

The spores of *Leclercqia* and the dispersed spore morphon *Acinosporites lindlarensis* Riegel: a case of gradualistic evolution

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SYNOPSIS. Variation in the spores of the lycopod *Leclercqia complexa* is described from the Middle Devonian of New York State, U.S.A. The spores are grouped into morphotypes forming a gradationary series representing two primary factors: ontogenetic maturity and natural variation. Comparisons are made with spores of *Leclercqia* sp. nov. from the upper Emsian of New Brunswick, Canada; with dispersed spores from various upper Emsian — lower Givetian localities; and with published records of *Acinosporites lindlarensis*. An inferred evolutionary lineage connects the two lycopod species, their spores, and dispersed spores of the *Acinosporites lindlarensis* morphon. These fossils show gradualistic evolution from the late Emsian to the early Givetian. *In situ* spores exhibit 'palingenesis': immature spores of *L. complexa* resemble the mature spores of *Leclercqia* sp. nov., thus connecting the two known plant/spore events in the *Leclercqia* lineage. Palynodemes have greater potential than miospore species alone for stratigraphical subdivision, because they represent temporally distinct records of individual plant species. The *Leclercqia* palynodemes exhibit two tendencies with time: a) curvatural spinae become larger, b) the proportion of spores with small distal sculpture decreases. The maturation sequence in *L. complexa* spores parallels the evolutionary history of morphotypes. Dispersed spores indicate that *Leclercqia* was widely distributed in late Emsian to Givetian times. *Acinosporites acanthomammillatus* and *A. macrospinosus* probably belong to related lycopods.

INTRODUCTION

Records of Devonian plants with *in situ* spores of complex structure and sculpture are becoming increasingly common. Spores of a monopseudosaccate spore genus, *Rhabdosporites* [*R. langii* (Eisenack) Richardson 1960], were first discovered in *Tetraxylopteris* (Bonamo & Banks 1967) and later, identical spores were found in another progymnosperm, *Rellimia* (Leclercq & Bonamo 1971, 1973). In contrast, the rhyniophytoid *Cooksonia pertonii* Lang 1937 (Fanning *et al.* 1988, 1992) has yielded crassitate spores belonging to four dispersed genera with different sculpture from two stratigraphical levels, the Upper Silurian (Downton Group +/- = Pridoli) and the Lower Devonian (Lower Ditton Group, lower but not lowest Gedinnian) of the Welsh Borderland. In the Downton Group, laevigate and verrucate spores, both with an equatorial crassitude, and belonging to the dispersed spore genera *Ambitisporites* and *Synorisporites* (*S. verrucatus* Richardson & Lister 1969) were found in the sporangia of *C. pertonii*. Associated spore masses (possibly of *C. pertonii*) contained structurally identical murornate spores with proximal papillae, *S. tripapillatus* Richardson & Lister 1969. The Lower

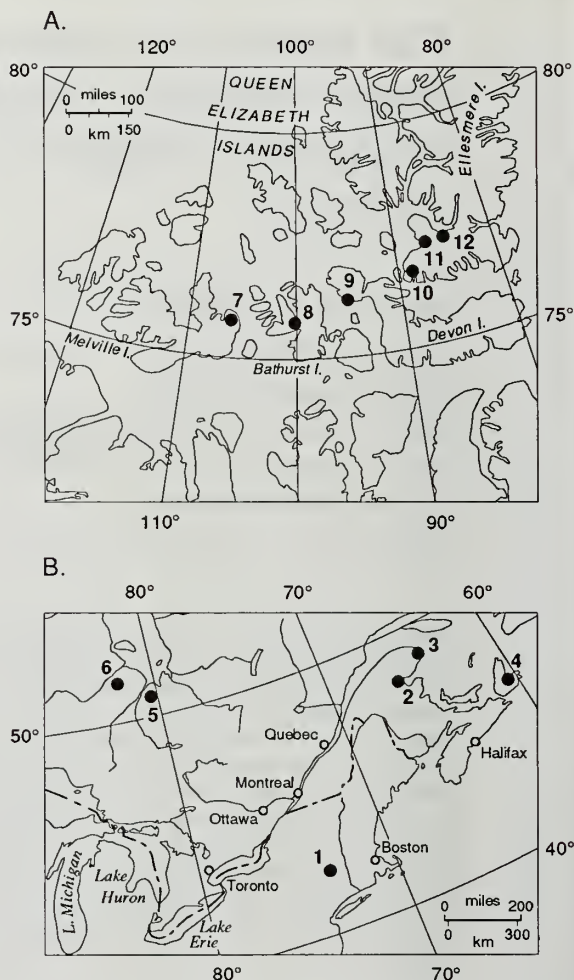
Dittonian spores of *C. pertonii* have the same structure but are apiculate and belong to the miospore genera *Streelisporea* and *Aneurospora*. The parent plants are apparently identical but their isospores, with similar structure, have dissimilar sculpture which changed through time from laevigate and verrucate-murornate to apiculate. A similar trend in sculpture is repeated in dispersed cryptospores and in miospores of several structural groups, from the Wenlock to the Gedinnian (Richardson & Burgess ms.). The earliest known trilete spores free from the tetrad appear in the Llandovery. They are laevigate with an equatorial crassitude (*Ambitisporites*) and are similar to some of the Downtonian spores of *C. pertonii*.

Leclercqia complexa Banks, Bonamo & Grierson 1972 and *Leclercqia* sp. nov. (Kasper unpublished) are more complex plants than *Cooksonia pertonii*. Some of the spores of *Leclercqia complexa* (lower Givetian) described below are closely similar to *in situ* spores in Kasper's material (upper Emsian) and can be placed in a single species of *spora dispersae*, whereas in *C. pertonii* four different dispersed spore genera occur in apparently identical plants of two different ages.

The importance of this and similar studies of *in situ* spores cannot be over-emphasized. In the thirty years since Nau-



Fig. 1 Maps showing provenance of specimens. 1 — New York State (Blenheim-Gilboa); 2 — northern New Brunswick (Dalhousie Junction); 3 — Gaspé, Quebec; 4 — northern Nova Scotia; 5 and 6 — northern Ontario; 7 — Melville Island; 8 — Bathurst Island; 9 — Devon Island; 10–12 — Southern Ellesmere Island. For additional information, see Appendix I, Register of Localities.

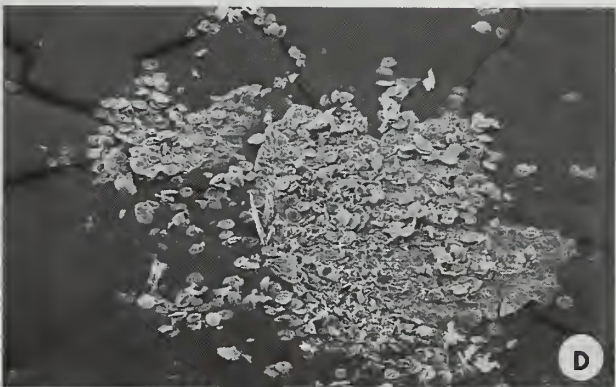
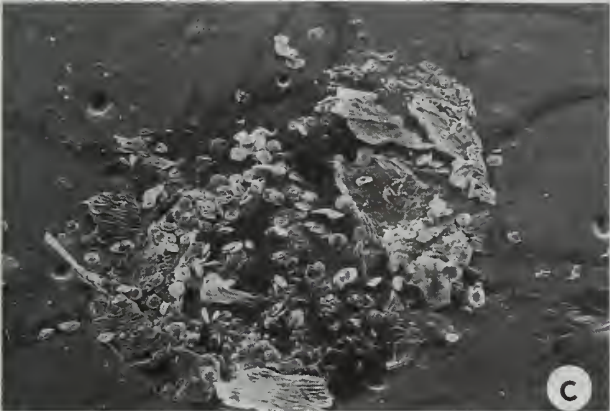
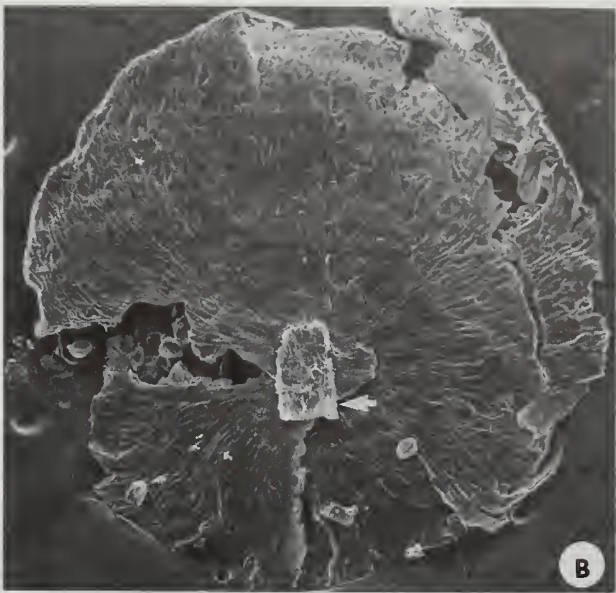
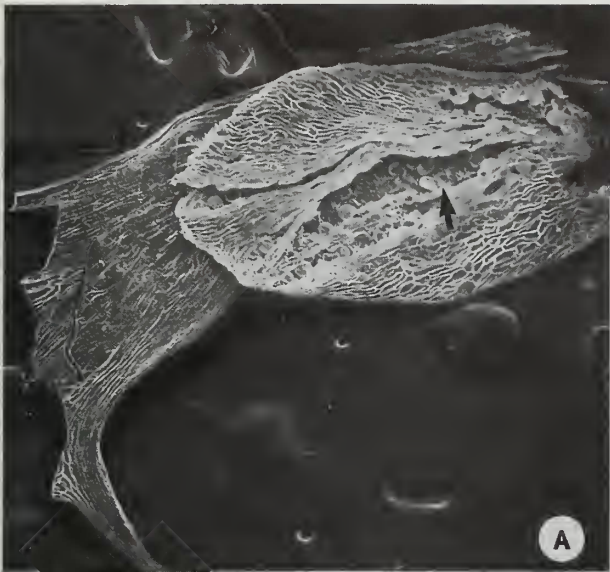


moa (1953) published her classic work on the dispersed spores of the Russian Platform there has been a tremendous increase in the amount of data on Devonian *spora dispersae* and their stratigraphical and geographical distribution. This information could, if better understood in an evolutionary context, vastly increase our knowledge of the evolution, distribution and habitats of Devonian land floras, all of which profoundly influenced the evolution of terrestrial animals (Shear *et al.* 1984). Dispersed spore records greatly exceed those of their parent plants, and the key to this treasure chest of data is the study of *in situ* spores: studies of the diversity of *in situ* spores and how they change in time may give clues to evolutionary pathways of dispersed spores and their parent plants which neither plants nor spores alone can give.

This paper describes the wide variety of spores present in numerous sporangia of two species of *Leclercqia*. The spores are easily identifiable in dispersed spore assemblages because of their distinctive, complex sculpture. Dispersed spores, many identical to those found *in situ*, were investigated from middle Emsian to lower Givetian strata of North America

and are considered to belong to one morphospecies. Within this species we describe 15 informal variants referred to numbered types and subtypes. This sequence of assemblages of types we regard as a single species morphon. A morphon has been defined as 'a group of palynological species united by continuous variation of morphological characteristics' (van der Zwan 1979, p. 11; see also van der Zwan & Walton 1981). As form taxa and taxonomic levels are subjective, we are extending the morphon concept to include groups of informal units at any taxonomic level that are interconnected by continuous variation. By our definition some morphons may be intraspecific. Within the intraspecific morphon of *Leclercqia* spores, and spores inferred to belong to this plant genus, the morphographic ranges and proportions of types vary through geological time. At a particular geological horizon, the pattern of types and subtypes constitutes a palynodeme (Visscher 1971) which may be unique in its range of variation. For example, the lower Givetian palynodemes represented by spores of *L. complexa* are composed mainly of various subtypes within Type I, whereas in the dispersed spore

Fig. 2 *Leclercqia complexa*, scanning electron photomicrographs of sporangia and spores from Blenheim-Gilboa. (a) Sporangium attached to sporophyll showing *in situ* spores (arrow), 101A, tilt 70°, $\times 40$. (b–f) One sporangium and its spores: (b) intact sporangium with portion of sporophyll attached eccentrically (arrow), 42A, tilt 60°, $\times 50$; (c) upper half of sporangium with spores of Subtype IC, 42A, tilt 90°, $\times 40$; (d) bottom half of same sporangium, 214, tilt 90°, $\times 40$; (e) detail of spore mass in (d) of Subtype IC spores, 214, tilt 45°, $\times 200$; (f) distal view of a single spore from (d) showing acanthomammillate distal sculpture, 214, tilt 22°, $\times 1,000$.



assemblages from the upper Emsian and Emsian/Eifelian the spores of the palynodemes belong to subtypes of V and VI (Table 1 and Fig. 18).

Our use of the term palynodeme requires some explanation. We have three types of spore data. The first two (*in situ* spores, and spores from a single horizon and geographical location, i.e. +/- contemporaneously dispersed spores) are regarded as true palynodemes *sensu* Visscher (1971). The third set of data is heterogeneous and derived from multiple samples collected at several locations and/or horizons, but within a limited stratigraphical range. In order to distinguish these types of data in the text, assemblages from multiple localities/horizons (Fig. 1 and Appendix I) are referred to as 'palynodemes', e.g. the middle Emsian 'palynodeme' (Hudson Bay Lowlands). In the Eifelian — lower Givetian 'palynodeme' (Canadian Arctic), material is sparse, was collected from several localities and belongs to two adjacent spore zones (see Table 1). Nevertheless, such dispersed spore assemblage data are remarkably consistent (see Table 1) and therefore are included in our lineage along with true palynodemes. Though this situation is far from ideal, the data presented, consisting of two lycopod species, their *in situ* spores, and dispersed spores of the *lindlarensis* morphon, represent one of the most complete plant/spore lineages in the pre-Quaternary record.

Photomicrographs were taken with a Leitz Ortholux microscope and Orthomat and an ETEC Autoscan B-1 SEM with polaroid PN-55 film at the University Center at Binghamton, State University of New York (SUNY-B); Zeiss Photomicroscopes II & III and a Hitachi 8S800 Field Emission SEM using HP5 film at The Natural History Museum, London, previously the British Museum (Natural History) (BM[NH]). Spores were coated with carbon and gold palladium or with gold palladium alone (SUNY-B) or gold (BM[NH]).

In the descriptions and the figure captions, the letter following each SEM stub number (e.g. 92K) refers to a particular sporangium. SUNY microslides (e.g. 2002 M 14) bear collection numbers (2002) followed by M for maceration and then a sample number (14). BM numbers (e.g. BM 051956 [334.1a]) refer to negatives in the archives in The Natural History Museum, London, and the number following in brackets is the specimen number from the Paleobotanical Collection, State University of New York at Binghamton. These 'BM' combination numbers refer to spores obtained from the matrix surrounding *Leclercqia*. Samples 334.1a, 1b, 1c refer to separate samples from a single large block consisting of a thin layer with large axes of *Rellimia* (1c) intercalated between two thick layers with abundant *Leclercqia* (1a, b). Dispersed spores from the Blenheim-Gilboa outcrop and borehole (B1, B2, & B3) sequences have a sample number added (e.g. BM 050053 [B1/24]). B1/24 refers to sample 24 from borehole B1. Dispersed spores from Canadian localities (Appendix I) are keyed to Geological Survey of Canada locality and slide numbers, (e.g. locality

A-008058/22) and those illustrated have been assigned GSC type specimen numbers (e.g. GSC 96756).

All these numbers and the microslide numbers for the dispersed and *in situ* spores are given in the figure captions or Appendix III. Locality information is provided in Appendix I. Figured specimens of SEM mounts from New York State are conserved in the type collections of the State University of New York at Binghamton. Dispersed spores from New York and Canadian localities are in the Canadian National Type Collection of Invertebrate and Plant Fossils at the Geological Survey of Canada, Ottawa.

BLENHHEIM-GILBOA (NEW YORK) — *LECLERCQIA COMPLEXA*

Material

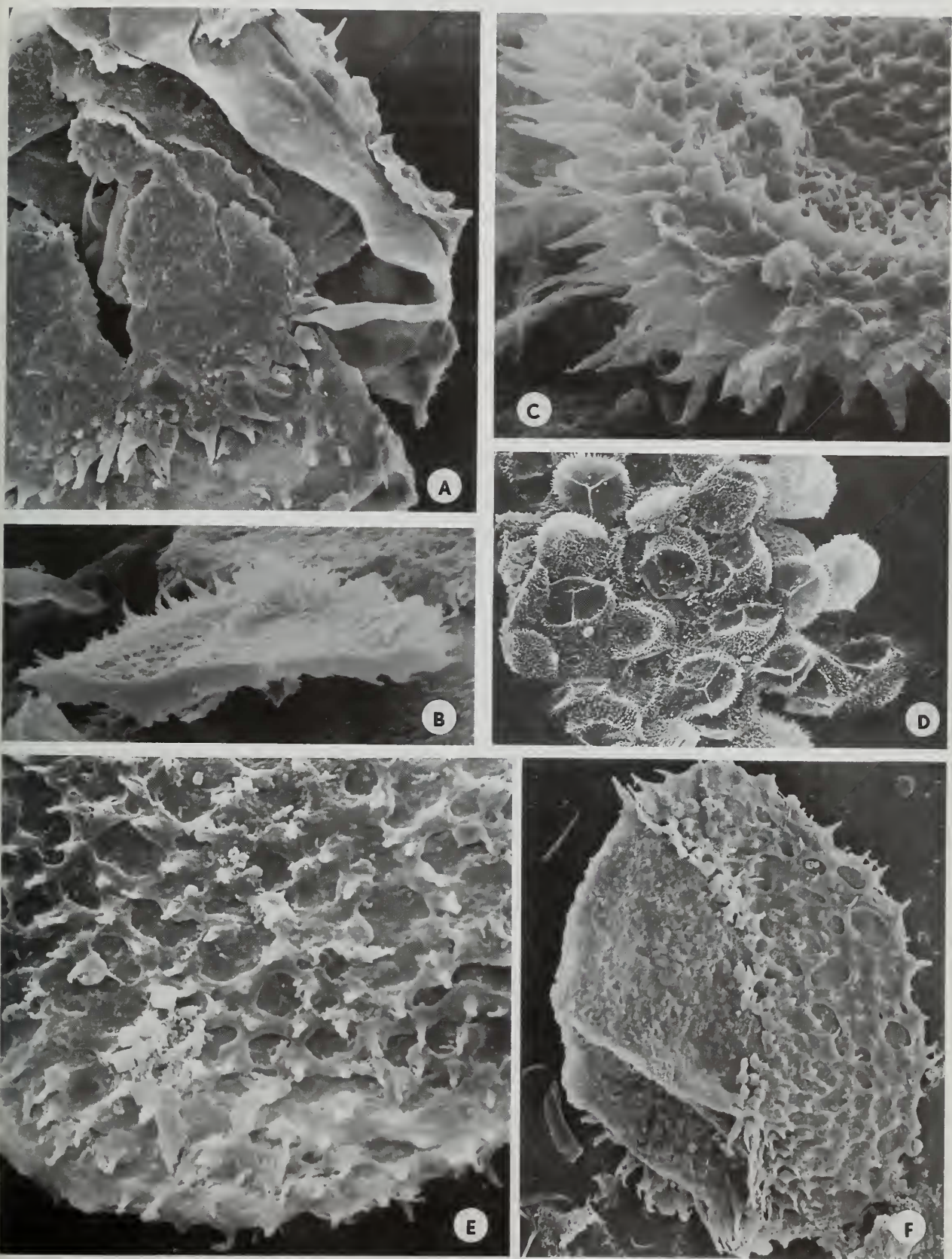
The present study of *in situ* spores is unique in that it is taking place in association with wide ranging studies on the geology, palaeontology, palaeobotany and palynology of marginal alluvial and marine sediments associated with the Catskill Alluvial Complex. Novel associations of arthropods and plant remains have already been revealed by this study (Shear *et al.* 1984, 1987, 1989a, b; Shear & Bonamo 1988; Norton *et al.* 1988; Kethley *et al.* 1989; Schawaller *et al.* 1991; Selden *et al.* 1991).

The locality data are given in Banks *et al.* (1972) for the original *Leclercqia complexa* locality at the Blenheim-Gilboa Pumped Storage Power Project. This site is now submerged by the lower reservoir. The additional localities sampled and discussed in this paper (see Appendix I) are: the cliff exposure behind the Power Plant and cores from borehole B1 drilled to a depth of 377.9 m and located 1143.8 m N60E of the reservoir near the Power Plant. The specimens are from the upper Panther Mountain Formation, Hamilton Group, Middle Devonian (Fisher *et al.* 1962, Rickard 1964, 1975). Our evidence for the age is discussed below.

Techniques for *in situ* spores

Small portions of sediment containing abundant *Leclercqia* axes were either transferred or macerated in hydrofluoric acid for three to four days, then given a hydrochloric bath for 24 to 48 hours. The material was neutralized by repeated washings with water containing a few drops of Kodak Photoflo. Photoflo, with a high pH, hastens neutralization and reduces the surface tension of the liquid, thus minimising the breakage of plant parts during manipulation. The resulting macerate was examined with a dissecting microscope. Even though the matrix appeared to contain only axes of *Leclercqia* with no intermixing of other genera, sporangia were chosen for further study only when their identity with *Leclercqia*

Fig. 3 *Acinosporites lindlarensis* and *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs; (a, f) dispersed spore; (b–e) *in situ* spores. (a) Equatorial view showing the two-layered structure of the exine, curvatural spinae and possibly vacuolate exoexine, BM 050056[B1/24], tilt 0°, × 1,700. (b) Equatorial view of broken spore showing 'homogenised' exine with distal and proximal exinal layers fused so that no lumen is visible, 214, tilt 45°, × 2,000. (c) Distal view showing typical evenly tapered curvatural spinae of Type 1, 42A, tilt 90°, × 3,000. (d–e) Subtype 1A spores derived from sporangium 91C: (d) part of a sporangial mass of spores of subtype 1A showing curvatural spinae, trilete ridges and closely packed distal sculpture, tilt 45°, × 200; (e) detail of distal sculpture showing lacunae and bifurc elements on muri, tilt 45°, × 2,000. (f) Equatorial view of Subtype 1A showing proximal, curvatural and distal sculpture, BM 051645 [334.1c], tilt 0°, × 1,200.



could be established either by their attachment to a sporophyll (Fig. 2a), or by their size and shape and the presence of an eccentric attachment pad (Fig. 2b; see also Bonamo *et al.* 1988).

Sporangia to be studied by light microscopy were first cleared one at a time in an embryological watch glass containing concentrated Schulze's solution (saturated solution at room temperature). Some sporangia were split in half or broken with needles to release the spore mass into solution. The clearing process was monitored under a dissecting microscope in a hood. Spores were removed with glass micropipettes, as they cleared, into a solution of Photoflo and water. After clearing (ca. 30 minutes) the spores and sporangial wall fragments were neutralised together in a watch glass by repeated washings with Photoflo and water, then mounted by micropipette on a coverslip in Clearcol. When the Clearcol hardened, the coverslip was affixed to a slide with Diaphane. Each slide contains hundreds of spores, all derived from a single sporangium.

Sporangia to be studied by scanning electron microscopy were also treated one at a time. They were removed from the neutralized macerate and placed on a stub with double sided Sellotape without clearing. Each sporangium was then teased apart with needles and the spores allowed to fall onto the tape. Thus sporangia and spores for SEM study underwent no acid or oxidative treatment other than that necessary to extract them from the rock matrix (HF/HCl). Several sporangia could be placed on one stub without intermixing the contents. The stub was numbered and each sporangium was given a letter designation (i.e. 92A designates stub 92, sporangium A). Some intact sporangia were first examined with the SEM (Fig. 2b) and then split in half. The portion originally fixed to the tape remained behind and was recoated (Fig. 2c); the other half was turned over and fixed to another stub (Fig. 2d-f). Thus stub 214 (Fig. 2d) supports the lower half and part of the spores of sporangium 42A (Fig. 2c). These methods permit comparisons of spores of the same and different sporangia.

Variation of *in situ* spores

Leclercqia complexa is apparently homosporous and has yielded spores similar to the dispersed spore species *Acinosporites lindlarensis* Riegel 1968. The three characteristic sculptural features of the spores are: i) a row of usually evenly tapered curvatural spinae (Fig. 3c) or biform tuberculae separating two types of sculpture differing mainly in size (Fig. 4a, 5a); ii) proximal sculpture of small interconnected elements that are sometimes biform (Fig. 3f, 6c, e, f); iii) variable distal sculpture with either 'beaded' muri or ridges (i.e. biform elements with slender mural interconnections) in a polygonal or irregular pattern (Fig. 4c, d), or sinuous and broad muri separated by rounded or irregular lacunae (Fig. 4a, b). The muri consist of basally interconnected biform elements. These sculptural elements have either expanded

bases and slender apical conical or spinae, or narrower bases surmounted by parallel-sided or tapered conical. When such interconnected biform elements are crowded together the resulting sculpture is referred to as acanthomammillate (Fig. 2f, 9a-d). Trilete sutures are covered by variably elevated unpaired lips (tectae) sculptured by small conical ($> 1\mu\text{m}$; Fig. 5a, f). A distinct inner body (intexine) may be seen under the light microscope. One broken specimen, in fracture section under the SEM, reveals a thin intexine separated, at least in part, from the outer exoexine which appears vacuolate (Fig. 3a). The lacunose nature of the surface of some specimens in plan and the slender connections between the sculptural elements, seen best in profile, may be a result of the partial degradation of a vacuolate exine. An intexine is not always visible and its presence or absence may be diagenetically controlled (cf. Fig. 3a, b). A fracture section (Fig. 3b) shows a 'homogenised' spore wall with both the exinal layering and the spore lumen obliterated. In spite of the considerable variation found, most spores conform to the circumscription of the dispersed spore species *Acinosporites lindlarensis*. Although the end members of the variants are distinct they are joined by a plexus of intergrading intermediaries.

The morphographic variation discussed below is mainly between the spores of different sporangia. Spores from an individual sporangium, numbering well over 1,000, commonly belong to a single type or subtype. This study is based upon more than 200 sporangia.

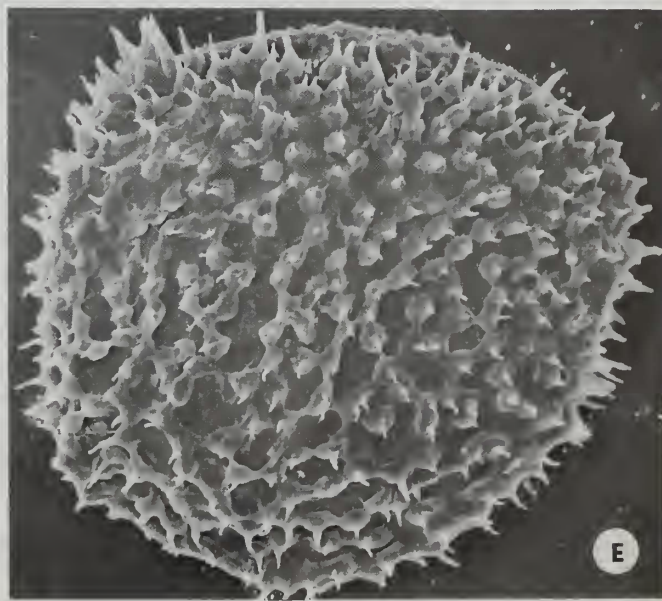
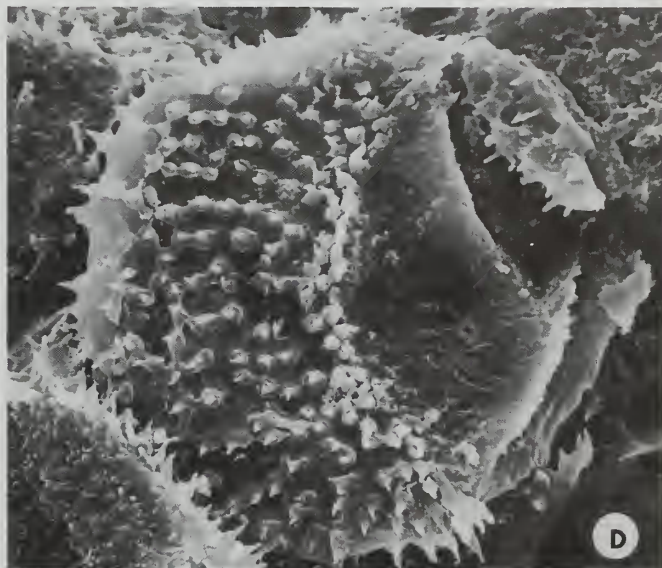
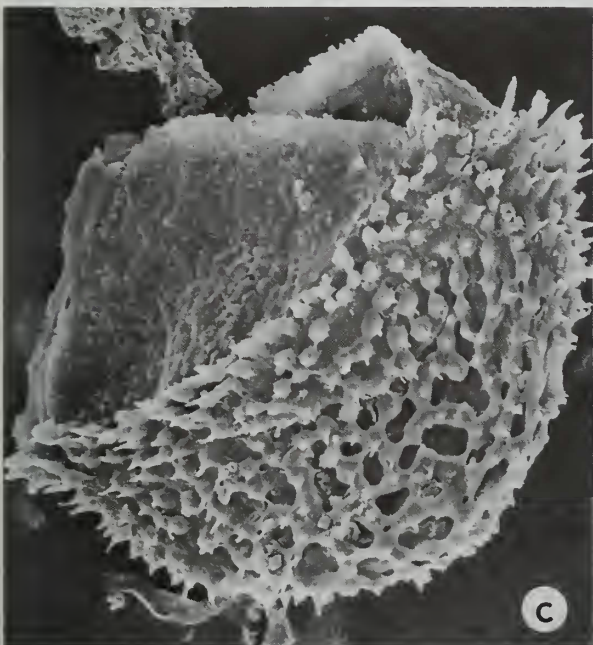
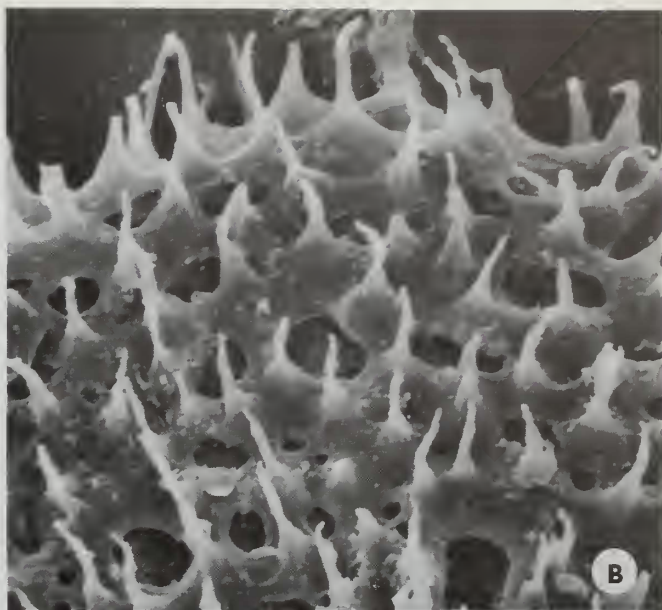
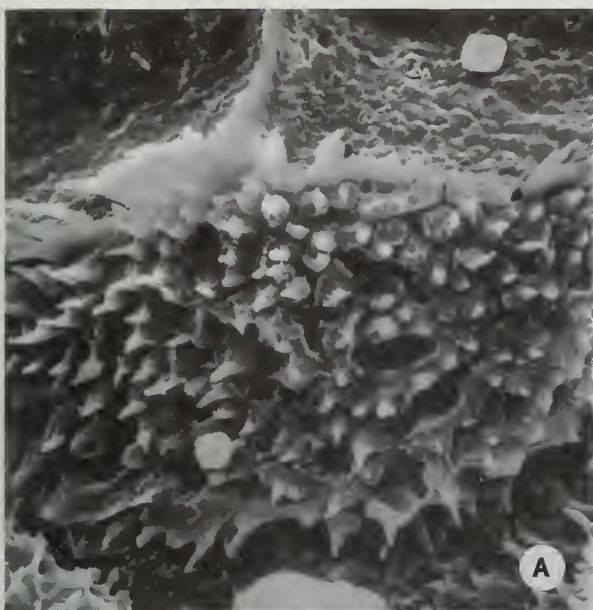
In assessing the range of variation, three factors have to be taken into account: 1) genetic variation; 2) ontogenetic variation (maturity); 3) preservational effects.

In situ spores described below show a number of basic features in common, but the variation is considerable and affects all three sculptural areas: proximal, curvatural and distal. The trilete mark is also variable and a central body is visible on some specimens. The spores have been arranged in six intergrading types and seven subtypes. The descriptions are based entirely on *in situ* spores, but when possible, dispersed spores from the rock matrix are included for comparison.

Type I. In most of the sporangia examined, Type I spores are dominant (Fig. 2c-f, 5e-f, 6a-f). The spores have relatively large (6–10 μm), uniformly tapered and pointed, curvatural spinae (Fig. 3c). The distal sculpture consists of biform elements (tuberculae surmounted by spinae) with coalescing bases (Fig. 4d) forming a variety of murornate patterns (Fig. 6b, 7b). The spinae over the distal surface of some dispersed Type I spores may include elements that have interconnected slender strands above the apparent spine bases (Fig. 5c, d). This feature may be preservational, related to degradation of a vacuolate outer exoexine. Proximal sculpture consists of small, crowded, biform elements. Type I is divided into three subtypes based primarily on their distal sculpture:

Subtype IA. The distal muri form irregular polygons

Fig. 4 *Leclercqia complexa* and *Acinosporites lindlarensis* from Blenheim-Gilboa, scanning electron photomicrographs; (a, d and f) *in situ* spores; (b, c, and e) dispersed spores. (a) Equatorial view of Subtype IA spore showing distal lacunae, 91C, tilt 45°, $\times 2,000$. (b) Detail of part of the distal exine of a variant of Subtype IA showing elongate, biform spinae and lacunae, BM 0519578 [334.1a], tilt 0°, $\times 4,000$. (c) Subtypes IA–B. Equatorial view, showing proximal trilete ridges, curvatural spinae and distal sculpture of muri surmounted by biform elements and surrounding lacunae. Distally the sculpture is like IA and subequatorially like IB, BM 051933 [334.1a], tilt 0°, $\times 1,300$. (d) Subtype IB equatorial view showing 'beaded' distal muri surmounted by biform elements, 91C, tilt 45°, $\times 1,000$. (e) Subtype IB distal view showing 'beaded' muri forming polygons surmounted by spinae and biform elements, BM 050076 [B1/24], tilt 0°, $\times 1,000$. (f) Variant of Subtype IC in equatorial view showing elongate spinose terminations on the biform elements, 7, tilt 90°, $\times 1,000$.



surrounding 'smooth' areas of the exine, or the muri are broad, not clearly differentiated, enclosing lacunae of variable size (Fig. 3e–f, 4a, 12a–c). Spinose terminations of the biform units may be elongate (Fig. 4b). This subtype intergrades with Subtype 1B, some spores showing ornament of both types (Fig. 4c). Proximally, the sculpture is reduced (Fig. 3f) and the trilete suture is covered by a low narrow ridge (tectum) sculptured by microcon (i.e. con $< 1 \mu\text{m}$).

Subtype 1B. The distal muri are 'beaded', i.e. the ridges are constricted between biform elements (Fig. 4d, 12d–f) and form irregular, sometimes incomplete, polygons (Fig. 4e). In sporangium 91C (Fig. 4d) the proximal sculpture is unclear, but some dispersed spores (Fig. 5a with SEM and slide 329/M/61 with light microscope) show well developed proximal sculpture and sculptured trilete ridges. Fig. 5a also illustrates evenly tapered curvatural spinae typical of Type 1 spores. Subtypes 1A and 1B can occur in the same sporangium, but 1B is rare.

Subtype 1C. The muri are sinuous but so crowded they obscure the lacunae and the murornate pattern (Fig. 5e, f, 6a, d). In sporangium 92B (Fig. 5e), only Subtype 1C is present. Stubs 42A and 214 (Fig. 2c–f) are also from a single sporangium and consist solely of Subtype 1C. These spores, like 1A and 1B, have biform sculptural elements consisting of tuberculae surmounted by slightly tapered to more or less parallel-sided slender con, spinae or bacula (Fig. 6a, b, d). Proximal sculpture is relatively large and biform, with minute bacula surmounting relatively large tuberculae that are interconnected at their bases (Fig. 6e, f). The unpaired lips (tecta) may form well-developed ridges sculptured by microcon (Fig. 5f). Subtype 1C may occur in loose tetrads.

Each of these subtypes, 1A, 1B and 1C, may include specimens having distal biform elements consisting of small tuberculae with elongate spinose terminations.

In one specimen, a variant of Subtype 1C, the distal tuberculae and spinae are elongated (Fig. 4f). This form may intergrade with typical 1C. Spores from sporangium 91D (Fig. 6b) show an acanthomammillate tendency in lateral compression, and in some specimens the spinose terminations are elongated but, in contrast to typical Subtype 1C, the wall is partially lacunose (see also 6c).

Type II. Most curvatural spinae are delicate and baculate, evenly tapered, or biform, and the distal sculpture consists of ridges that are only slightly elevated.

Subtype 1IA. The distal spinae are slender, baculate to slightly tapered, and supported by low ridges (Fig. 7a–c, f) with irregular lacunae (Fig. 7d). Some specimens are reticulate (Fig. 7b). Sporangium 101A contains some spores transitional between Types I and II. On typical Type II spores the curvatural elements consist of either tuberculae (Fig. 7c), some of which appear biform, or delicate slender spinae; other specimens in the same sporangium have prominent, evenly tapered, elongate curvatural spinae like Type 1C (Fig. 7e). The proximal sculpture is apiculate to granulate, with elements similar to the other types, including Kasper's material described below. Some of the proximal elements are

biform. Laesurae are covered by weakly developed ridges (tecta, Fig. 7a).

?Subtype 1IB. Distal sculpture consists of stout biform elements on low ridges (Fig. 7g). Only one spore of this type was seen in this sporangium (92K) but a similar spore was seen in sporangium 92H.

Type III. The spores have slender curvatural spinae (Fig. 8a), and distal sculpture of grana (Fig. 8b), con or pointed spinae on barely discernible ridges. The ridges form an irregular, reticulate pattern, or are separated by oval to irregular lacunae (Fig. 8a, c). Some spores have larger distal sculpture. Sporangium 169A contains some spores similar to Type II and one specimen in distal view (Fig. 8d) showing biform con and ridges making polygons similar to Type I.

Type IV. Specimens of Type IV have distal sculpture like that of Type III, but longer curvatural spinae (Fig. 8e; 5–7 μm compared with ca. 1.5 μm on Type III). These specimens occur in the same sporangium as the Type III spores illustrated in Fig. 8a.

Type V. These spores have crowded, acanthomammillate distal sculpture and small, evenly tapered, or occasionally biform curvatural spinae. In the Blenheim-Gilboa sporangia, spores of this type are found only as tetrads, except for two specimens of Subtype VA separated from the sporangial mass.

Subtype VA (Fig. 8f, 9a). Curvatural spinae, seen on a few specimens only (Fig. 9b, arrow), are evenly tapered, tend to be small and may be biform. The proximal surface, rarely seen, bears reduced grana; no biform elements have been seen. Distal sculpture consists of crowded, smooth, sinuous ridges made up of biform elements of more or less equal diameter (Fig. 9c–d); ridges may be beaded but not crowded (Fig. 9d); biform elements consist of rounded bases (tuberculae) surmounted by slender con or spinae. The trilete mark, simple sutures or low ridges, is rarely seen.

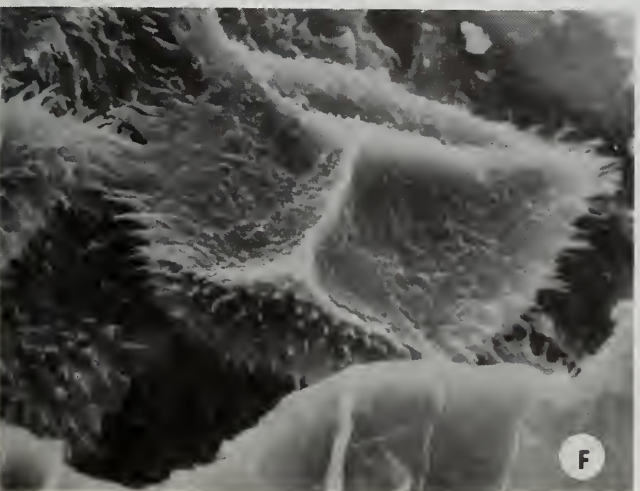
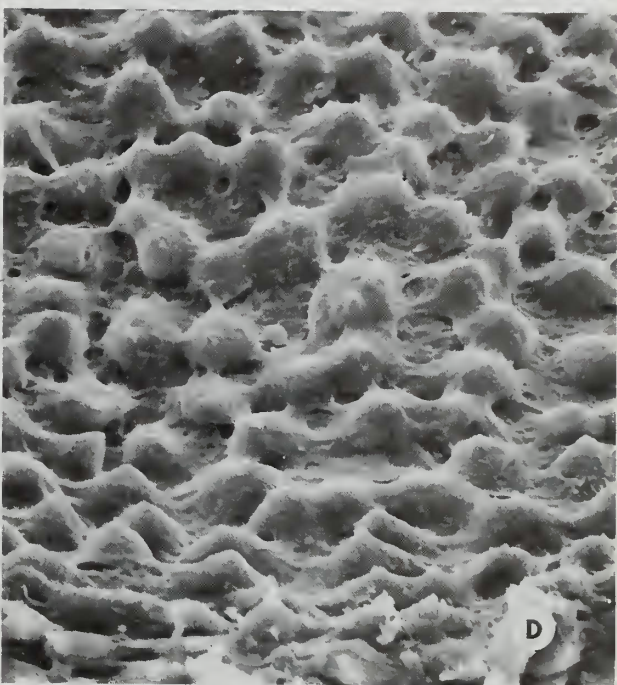
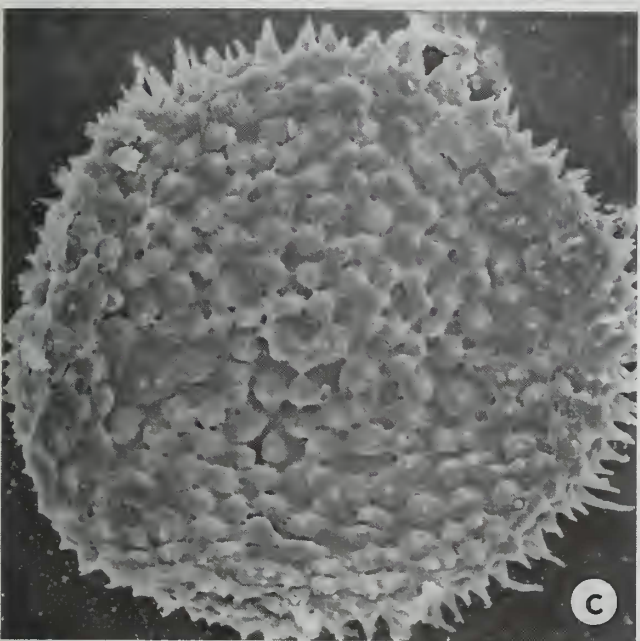
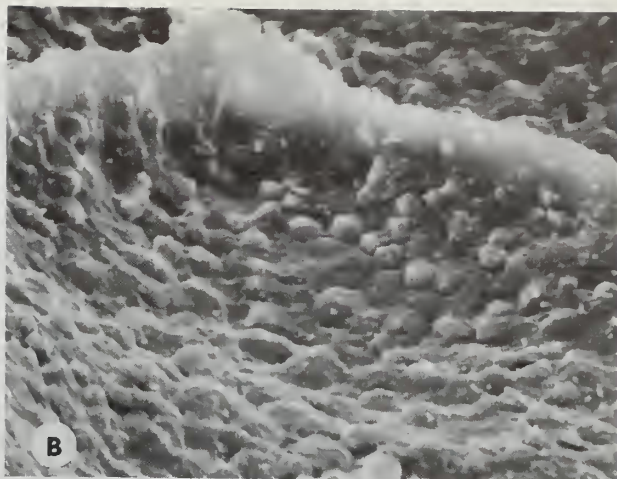
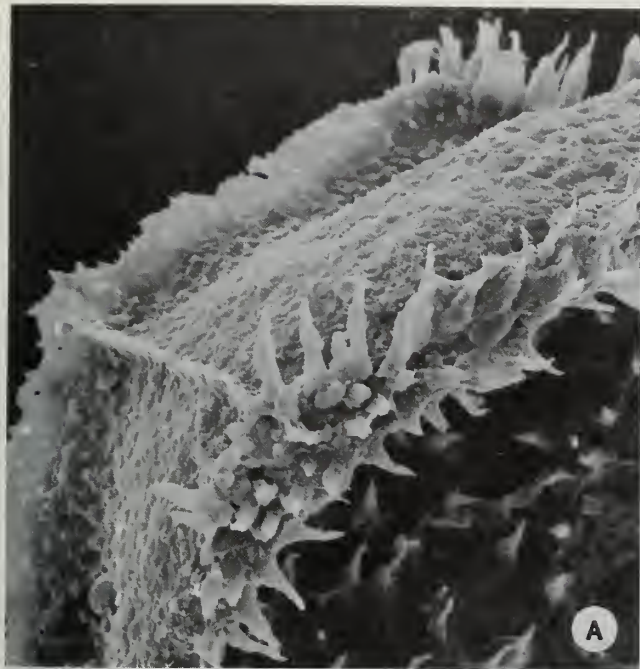
Subtype VB. The distal sculpture is smaller than in VA but is otherwise closely similar. The terminal con of the biform elements are shorter over the distal pole than in the subequatorial region (Fig. 9e). In some tetrads the spinae are more elongate and are similar to Type VI (Fig. 9f). No trilete mark was seen.

Type VI. Spores occur only in tetrads (Fig. 13 a–c). Distal sculpture consists of small, crowded, biform elements, with slender, variable, elongate spinae but is otherwise similar to that of Subtype VB; muri faint or indiscernible. The sporangium is smaller than for other types. The trilete mark was not seen.

Variation of dispersed *Acinosporites lindlarensis*

Two kinds of material were examined: firstly, spores from bulk maceration of the matrix of *Leclercqia complexa* and from immediately adjacent sediments; secondly, spores dispersed in nearly 400 m of strata from the Blenheim-Gilboa Borehole (B1), penetrated to a depth of 377.9 m, and in outcrop sequences.

Fig. 5 *Acinosporites lindlarensis* and *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs; (a–d) dispersed spores; (e–f) *in situ* spores. (a–b) Subtype 1B: (a) equatorial view, detail of proximal face showing sculptured, simple, trilete ridges, BM 051652 [334.1c], tilt 0°, $\times 2,200$; (b) oblique view, detail of proximal polar apex showing simple trilete ridges and biform elements, BM 050053 [B1/24], tilt 45°, $\times 4,000$. (c–d) Subtype 1C, distal polar view: (c) showing close-packed interconnected ridges, BM 050041 [B1/24], tilt 0°, $\times 1,500$; (d) detail of distal polar area of same specimen showing interconnected biform elements and microfoveolate nature of some of the interconnections, BM 050045 [B1/24], tilt 45°, $\times 3,500$. (e–f) Spores from sporangium 92B: (e) part of a sporangial mass consisting entirely of Subtype 1C spores, tilt 45°, $\times 300$; (f) detail of a spore in oblique proximal polar view, tilt 45°, $\times 1,000$.



An analysis of 133 spores picked out during bulk macerations of the rock matrix around *Leclercqia* from the Panther Mountain Formation gave the results illustrated in the first data set of Table 1.

The data in Table 1 may represent some selection by the observer (but see below) and may also be affected by the clearing techniques. Type I is dominant, Type V is absent and types II, III, IV and VI are rare, doubtfully present, or absent. Among the spores isolated from the sporangia, spores of Type I are dominant with Subtype IA most frequent among the subtypes.

Specimens of *A. lindlarensis* occur throughout the sequence of the Blenheim-Gilboa outcrop and borehole samples but are rare. They are abundant in the rock matrix surrounding specimens of *Leclercqia*. Subtypes IA and IB are numerically dominant among the spores found in both the matrix surrounding *Leclercqia* and in the borehole and outcrop samples. Subtype IA is dominant in all slides of specimens cleared during bulk macerations of *Leclercqia*, except one in which over half the specimens belong to Subtype IB. Consequently, all the dispersed spore evidence is consistent with that from the *in situ* spores.

Morphotype inter-relationships

Suggested ontogenetic relationships between spore types are shown in Fig. 10. Types V and VI are found only in tetrads, and such spores are immature both in size and sculpture. The sculpture in Subtype VB and Type VI is smaller than in Subtype VA. Therefore, the spores VB and VI are assumed to be the most immature. In VA the distal sculpture consists of crowded, smoothly sinuous to beaded ridges, in part formed of biform elements (acanthomammillate) and sometimes interconnected by slender muri. This sculpture is closely similar to that of Subtype IC which sometimes occurs in loose tetrads.

Specimens of Type I are considered to include the most mature spores for three reasons. Firstly, they are the commonest spores found on bulk maceration of the *Leclercqia* matrix. Secondly, Subtype IA is also the most common subtype of the *in situ* spores. Thirdly, the spores of Type I include the largest specimens, and they are usually found in the largest sporangia which are partially dehiscent.

Differences between Subtypes IA, IB, and IC may represent stages in maturation, natural variation, or preservational degradation. We consider that all three factors are involved, e.g. the differences between IA and IC may be due to a combination of maturity and degradation. In Subtype IC the distal sculptural elements are closely packed, whereas in Subtype IA the muri are separated and their elevation enhanced into the typical lacunose — reticulate pattern. At least two factors may be involved in this process: 1) swelling of the spore separating the bases of the muri and biform elements and 2) degradation of the intervening vacuolated outer layer of the exoxine. The exine pattern produced by the latter process indicates a structural control within the exine. The extension of these two tendencies plus the further

expansion of the spore would result in the further separation of the ridges as seen in Subtype IB.

There is no evidence that Types II, III, IV and VI of *Leclercqia complexa* were ever dispersed. Types II, III and IV have poorly developed ridges and biform elements and may be immature forms. Spores of Type VI intergrade with VB and are regarded as the most immature spores in our normal maturation sequence (Fig. 10). As the sculpture in Types II, III and IV is less well developed than in Type V, and the spores have separated from tetrads, other factors may have controlled their development. Perhaps in such spores separation from a tetrad occurred before full development of the sculpture. There is some similarity between the distal regions of Types II and III and the distal polar exines of Types VC and VD from New Brunswick (p.134; Fig. 11a, b; Fig. 17a) in which the ridges are not developed and the spinae arise from a foveolate (i.e. not ridged) exine. Alternatively, some of these types may represent mature spores of natural small-sculptured variants. Type III has slender curvatural spinae, and in Type IV these spinae are stouter.

Are these spores (II, III, IV) normal but immature genetic variants, or do they represent the products of abnormal development within the sporangium? The fact that these specimens are rare in dispersed assemblages may indicate that such spores are not normally dispersed in upper Eifelian — lower Givetian assemblages. Subtypes of V and IC are either tetrads or are considered as developing spores held within an immature sporangium. The spores may not be dispersed until the sporangia are ripe and contain Type I (A–B) spores. The occurrence of other types in the *Leclercqia* samples may be due to the presence of sporangia that have been crushed to reveal immature spores.

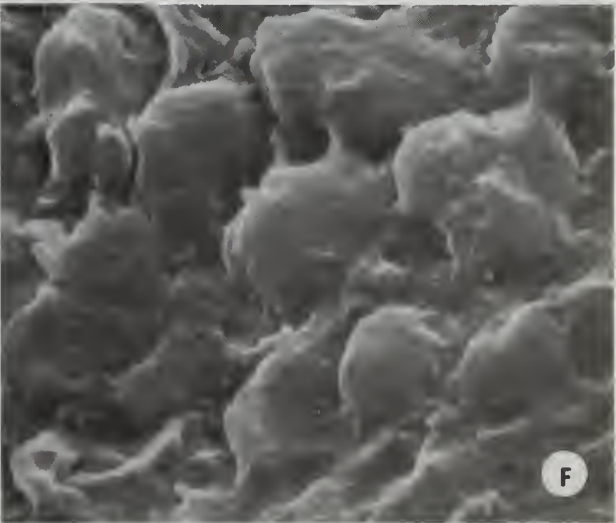
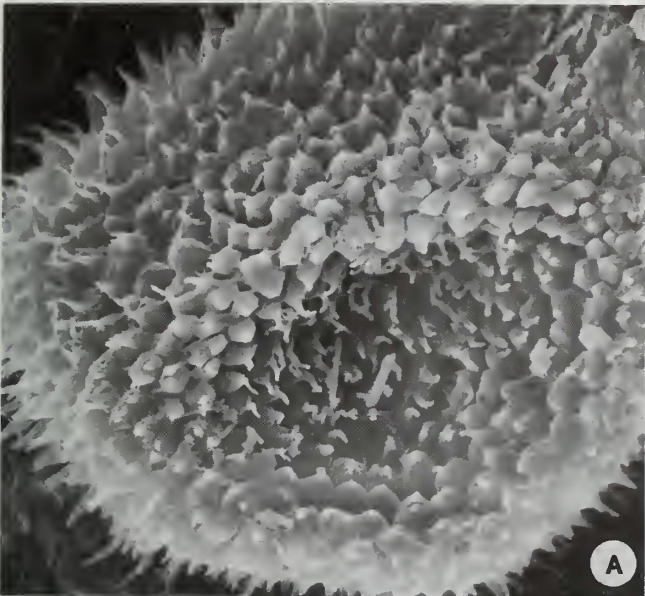
Forms with small sculpture may represent primary variants (Fig. 7a–d) [Type II, 101A]. These varieties are rare (see Table 1), but Type II is more common in older assemblages. The tendency to produce such spores is herein referred to as the 'parvulus' tendency.

One *in situ* specimen of Type I (Fig. 4f) was found with elongate tuberculae and spinae. It could be the result of natural variation, but similar spores have not been found in either the picked *Leclercqia* sample or the bulk macerated samples.

In situ and dispersed spores: structure, sculpture and nomenclature

STRUCTURE. All the *in situ* and dispersed spores appear to be azonate, but some show a variably separated intexine. Fracture sections give no indication of an equatorial or curvatural thickening. In some fracture sections (Fig. 3b), the proximal and distal parts of the exine are fused, and show no exinal stratification or lumen. In other broken specimens (Fig. 3a), a separated inner body (intexine) is present. Homogenisation owing to diagenesis may account for the apparent absence of an intexine in some of the New York specimens. Alternatively, these spores may be immature, and the presence of a

Fig. 6 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores, Subtype IC. (a) Distal view showing crowded biform elements, 92B, tilt 45°, × 2,000. (b) Equatorial view showing crowded distal biform elements with elongate terminal spinae, 91D, tilt 45°, × 1,000. (c) Tipped specimen showing trilete ridges, curvatural spinae and distal sculpture. Terminations of biform elements show little or no taper and are elongate, 45E, tilt 90°, × 1,000. (d) Equatorial view, showing crowded distal sculpture and long, evenly tapered curvatural spinae, 42A, tilt 0°, × 1,000. (e) Proximal apex showing trilete ridges and biform sculptural elements fused in groups, 214, tilt 45°, × 7,000. (f) Detail of proximal biform elements, 45E, tilt 90°, × 10,000.



body may characterize later stages of spore maturation.

In the dispersed and *in situ* spores prepared for light microscopy, oxidation may facilitate observation of the intexine. In order to evaluate these alternative interpretations, the dispersed spores of *Acinosporites lindlarensis* were compared with those *in situ*. In some of the preparations made for light microscopy, specimens showing a body were common. Preservation, maturation and oxidative treatment probably collectively determine whether or not the inner layer of the exine is observed. Some fractured specimens show a thin inner layer of the exine sometimes folded, and a thicker, structured outer layer that appears vacuolated under the SEM. These spores are regarded as azonate with an inner body (intexine) that is probably only attached proximally.

SCULPTURE. Equatorial and subequatorial spinae form a distinct, arcuate line joining the ends of the Y-rays, marking the edge of the contact areas and the position of the curvaturae perfectae. On most of the spore types these spinae are commonly evenly tapered, whereas most of the distal and subequatorial sculptural elements are biform. Specimens of Types IV and V, however, have shorter curvatural spinae, and some of these tend to be biform. A similar short-spined variant of *A. lindlarensis* var. *lindlarensis*, of early Givetian age, is figured by McGregor and Camfield (1976, pl. 5, figs 2, 3).

NOMENCLATURE. Streeel (1972) placed spores from the rock matrix around *Leclercqia complexa*, and 'identical to the spore produced by this lycopod' (1972, p. 205), in the dispersed spore genus *Aneurospora*. However, we interpret these spores as azonate and believe they are best excluded from *Aneurospora*. Because some spinae 'bear a "cupule-like" thickening' at their apex, Streeel (1972, p. 210) compared the spores with *Acanthotriletes heterodontus* Naumova 1953. Expansions of the spine tips have been found rarely in the present study. Except for the more common occurrence of the 'cupule-like' thickenings reported by Streeel (1972), his spores are identical to *Acinosporites lindlarensis*.

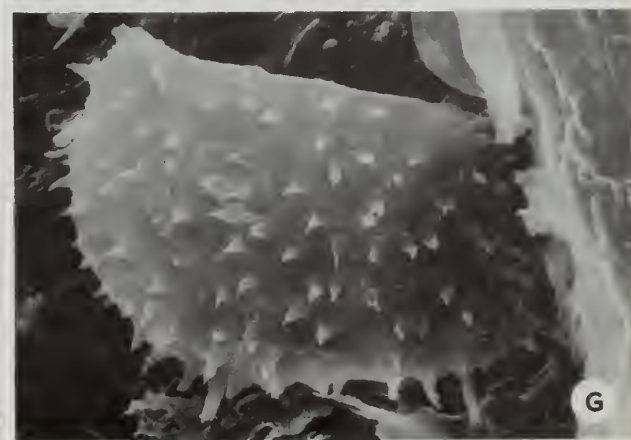
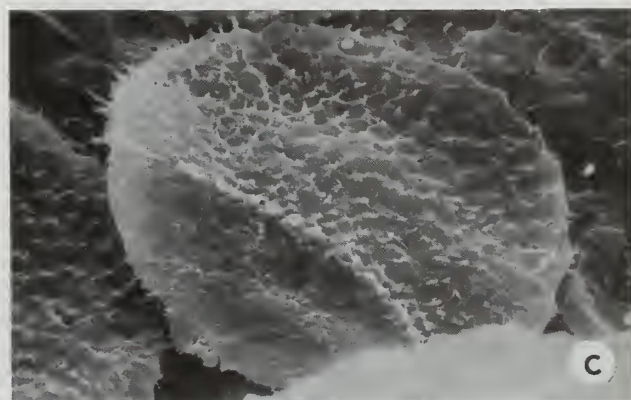
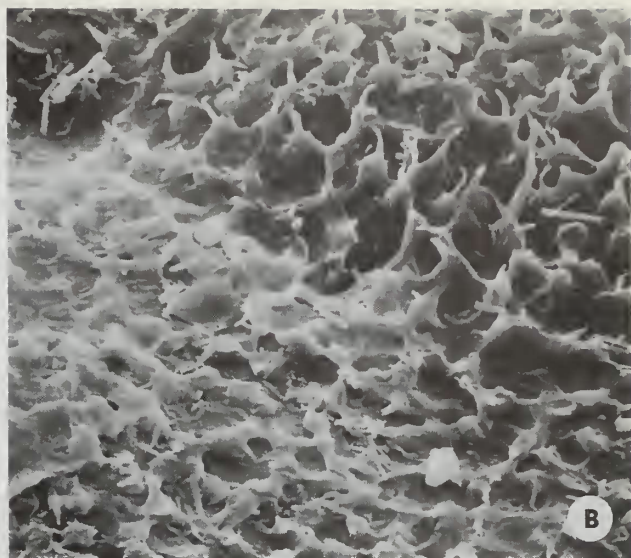
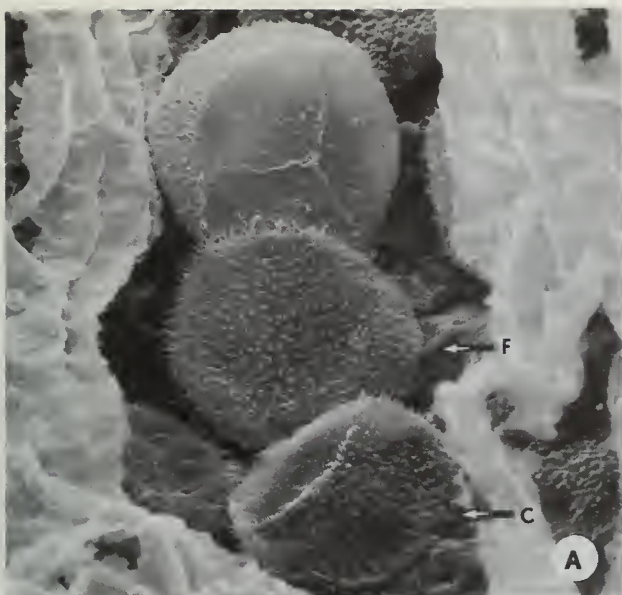
A distal sculpture of ridges with superimposed coni, spinae, or biform elements is the main feature of the genus *Acinosporites* and curvatural spinae are characteristic of *A. lindlarensis*. Riegel (1973) erected a second taxon, *Geminospora treverica*, for similar spores characterised by an intexine. McGregor and Camfield (1976) could find no difference between *A. lindlarensis* and *G. treverica*, and combined them. By establishing the variety *A. lindlarensis* var. *minor*, they also created the autonym *A. lindlarensis* var. *lindlarensis*. The type of the autonym is that of *A. lindlarensis* Riegel. *A. lindlarensis* var. *lindlarensis* has a known stratigraphical range from the middle Emsian to the middle Givetian.

Age of *Leclercqia* samples

Few long late Eifelian to early Givetian sections dated by other fossils and investigated palynologically, are available for comparison with the Blenheim-Gilboa sequence. Palynological dating of sequences of this age is further complicated by possible regional differences in spore assemblages. There are inconsistencies in the records of the first appearance of certain spore species between Arctic Canada and the Russian Platform on the one hand and between eastern North America and western Europe on the other (McGregor 1981, Richardson & McGregor 1986). Some of the differences involve key miospore events such as the incoming of *Samarisporites triangulatus* Allen 1965 and the 'flood' of *Geminospora* species (Richardson & McGregor 1986). At present the best conodont control of mid-Devonian spore sequences occurs in western Europe (Loboziak & Streeel 1980; Loboziak *et al.* 1991), but in that region there are gaps in the spore succession, particularly in the Upper Eifelian. Sections from the Soviet Union (e.g. Arkhangel'skaya 1985b) and long sections in Arctic Canada (McGregor & Camfield 1982; McGregor *in press*) provide more nearly complete stratigraphical sequences but with less faunal control. The question is further complicated by the possibility of variations in the geographical occurrence of *Geminospora* caused by local, and possibly regional, environmental controls.

Loboziak and Streeel (1980) have reported miospores from the Boulonnais, northern France. Their lowest assemblage, from the lowermost Blacourt Formation in Griset Quarry, contains poorly preserved specimens of several taxa in common with the upper part of the *devonicus-naumovae* Zone and the overlying *lemurata-magnificus* Zone. This lower Blacourt Assemblage is Givetian, according to associated conodonts. It is closely comparable to assemblages from the lower Blenheim sequence, which we believe are high in the *devonicus-naumovae* Zone. Spores from the middle and lower parts of this zone are not known in France. However, in several areas, Scotland (Richardson 1965 and unpublished), the Eifel (Riegel 1982) and Arctic Canada (McGregor and Camfield 1982; McGregor *in press*), more extensive sequences of the *devonicus-naumovae* Zone exist. In the Eifel region the uppermost Nohn to Freilingen formations correspond with the lower and middle *devonicus-naumovae* Zone (early to late Eifelian), whereas the overlying Ahbach Formation contains spores of the upper *devonicus-naumovae* Zone (Riegel 1982, fig. 1). *Geminospora lemurata* has now been found in two samples in the upper part of the Ahbach Formation, Müllert Member, just above the appearance of *Polygnathus ensensis ensensis* (Loboziak *et al.*, 1991). We therefore conclude that the Blenheim-Gilboa sequence is no older than late Eifelian (approximately middle *ensensis* conodont Zone of Ziegler 1979, fig. 6; *ensensis-obliquimarginatus* Zone of Loboziak *et al.* 1991, fig. 5).

Fig. 7 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores. (a-f) Subtype IIA, sporangium 101A; (g) Subtype IIB, sporangium 92K. (a) Enlargement of specimens at arrow in Fig. 2a. Spores within the sporangial wall, showing small, slender, curvatural spinae, weakly developed trilete ridges and small distal sculpture, tilt 90°, × 500. (b) Distal sculpture, showing weakly developed muri, surmounted by slender biform spinae and forming an irregular reticulate pattern, tilt 90°, × 2,000. (c) Enlargement of Fig. 7a, arrow c. Equatorial view showing weakly developed distal spinae and small distal sculpture, tilt 90°, × 1,000. (d) Distal view of spore showing lacunae, tilt 0°, × 1,100. (e) Transitional form similar to Subtype IC with well-developed curvatural spinae but smaller distal sculpture, tilt 45°, × 1,000. (f) Enlargement of specimen in Fig. 7a, arrow f. Detail of distal exine showing small lacunae and biform elements, tilt 0°, × 2,000. (g) Spore fragment showing low distal muri (ridges) and small, stout, biform elements and tuberculae, tilt 45°, × 1,000.



Brachiopod evidence from the Blenheim-Gilboa sequence indicates a late Givetian age (G. R. McGhee pers. comm.). Such a young age is not acceptable on palynological grounds.

A detailed account of the spore sequence at Blenheim-Gilboa will be published separately.

DALHOUSIE JUNCTION (NEW BRUNSWICK) — *Leclercqia* sp. nov.

Material

Plants belonging to a new species of *Leclercqia* with *in situ* spores have been discovered in the Campbellton Formation at GSC locality O-096376, 0.5 mile (0.8 km) west of Dalhousie Junction, New Brunswick (Kasper 1977). Comparisons between the New York and Dalhousie plants are limited because only a small amount of New Brunswick material is available. Plant material from this area was provided by Kasper who will publish details of his new species separately.

Variation of *in situ* spores

The following description is based upon the spores of only a few sporangia. The distal ornament of these spores closely resembles that of Type V from the Blenheim-Gilboa locality, but the curvatural sculpture is different.

Subtype VC (Figs. 11a-d, 17a, b). The spores bear typical acanthomammillate distal sculpture (cf. Blenheim-Gilboa Subtype IC and Subtype VA-B tetrads) of variably packed ridges, surmounted by small coni or biform coni and separated by lacunae (Figs. 11a, c, 17b). Alternatively, individual biform elements may be connected into irregular groups, consisting of a basal part with tapered sides, in profile, and surmounted by sharply tapered coni. In some specimens there are no ridges over the distal pole (Figs. 11a, e, 17a), but the exine is foveolate and supports slender coni or spinae; ridges occur towards the equator and appear beaded and markedly biform, but still crowded (Figs. 11b, d, 17a); distal subequatorial elements may be smaller and more crowded than those nearer to the distal pole. No evenly tapered curvatural spinae have been observed (compare with Fig. 9b of Blenheim-Gilboa) and the curvaturae are usually marked by a line of stout, rounded, weakly biform elements (Fig. 11b); sometimes these elements consist of a rounded, broad base bearing two coni or spinae. Proximal sculptural elements are smaller, crowded with polygonal bases and often distinctly biform (Fig. 11a). Tecta form low ridges sculptured by elements identical to those on the proximal face.

Subtype VD (Fig. 16a-d). Many specimens show a few biform curvatural elements with extended spinae that are larger than the distal biform elements (Fig. 11f, arrow, 16c) and are referred to as Subtype VD. The proximal sculpture is more prominent than that of Type V of the Blenheim-Gilboa material and consists of grana or tuberculae, many of which are biform. Proximal elements decrease in size towards the proximal pole. The trilete mark usually forms a low ridge on the exoxine (tectum) and lips or folds on the intexine (Fig. 11g) and in some specimens consists of simple sutures (Fig. 17c-d).

Variation of dispersed spores

The matrix surrounding *Leclercqia* sp. nov. and rock from other levels in the Campbellton Formation (see below), contains dispersed specimens of *Acinosporites lindlarensis*. Most of the spores show sculpture (Fig. 17d) closely similar to the acanthomammillate type seen in the *in situ* spores. In others, (Fig. 16f) the sculptural elements are more separated and approach those seen in Subtype IA. Small, elongate, biform curvatural spinae occur on some specimens from GSC locality O-096376. Proximal sculpture is well-developed and consists of scattered grana, sometimes interconnected into groups. The trilete mark consists of either simple sutures or trilete folds.

Age of *Leclercqia* sp. nov.

Dispersed miospores belonging to the lower *douglastownense-eurypterota* Assemblage Zone have been recovered from the beds containing *Leclercqia* sp. nov. (McGregor unpublished). The age of the plants is therefore late Emsian.

Comparison with the maturation sequence of *in situ* spores from Blenheim-Gilboa

Spores from near Dalhousie Junction resemble those of Type V from Blenheim-Gilboa. Among the dispersed spores are some with curvatural spinae that are mainly small and biform. The distal sculpture varies from that typical of Type V to a variety resembling Type IA, where the distal elements are arranged in small polygons. A further variant (Fig. 16f) was found with small distal sculpture of sinuous muri and biform elements ('parvulus' tendency). If our maturation sequence is correct (Fig. 10, p.138), *in situ* spores of *Leclercqia* sp. nov. most closely resemble, at least distally and equatorially, immature *L. complexa* spores that occur in tetrads. The dispersed spores from Dalhousie Junction show greater signs of development in terms of the proposed maturation series from Type VI, through V, to Subtype IA, but curvatural spinae are small and biform and not as well-developed as in IA.

DISPERSED SPORES OF THE *ACINOSPORITES LINDLARENSIS* morphon

In our palynological preparations

Dispersed specimens of *Acinosporites lindlarensis* have been examined from the following strata (see Fig. 1 and Appendix I): (a) Panther Mountain Formation, New York (see p.130 above); (b) Campbellton Formation, northern New Brunswick (samples collected by DCM and samples supplied to DCM by P.G. Gensel, J.D. Grierson and A.E. Kasper); GSC locality O-095530, *annulatus-sextantii* Assemblage Zone, middle Emsian; GSC locality O-098401, upper *annulatus-sextantii* Assemblage Zone, late Emsian; GSC localities O-096376, O-096385, O-098402, O-098403, and O-098404, lower *douglastownense-eurypterota* Assemblage Zone, late Emsian; (c) Battery Point Formation, Gaspé, Quebec (McGregor 1977); GSC locality A-007102, upper *annulatus-sextantii* Assemblage Zone, late Emsian; GSC localities A-005368 and A-007115, lower *douglastownense-eurypterota* Assemblage Zone, late Emsian; (d) Stopping River Formation, northern Ontario (McGregor & Camfield 1976); GSC

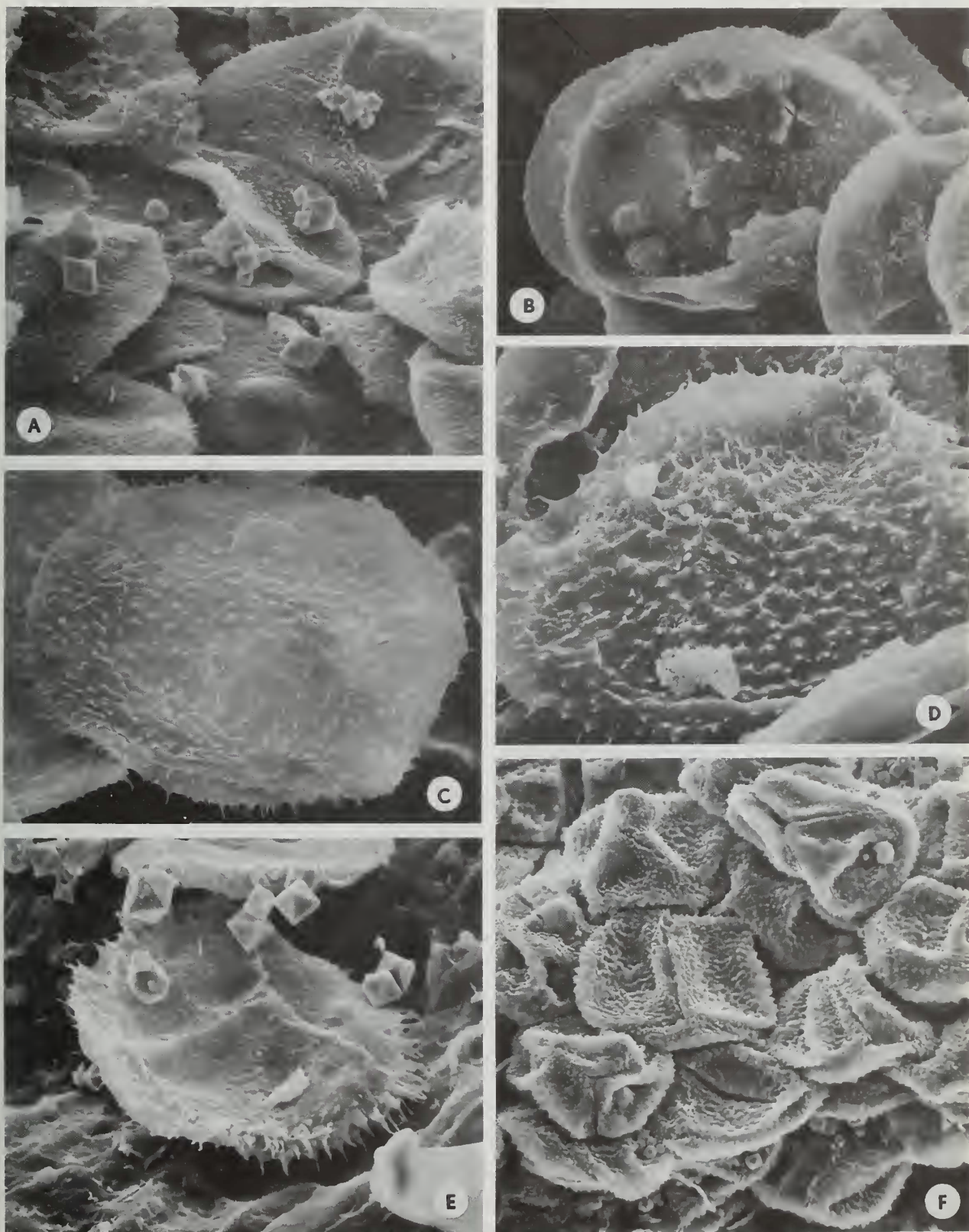


Fig. 8 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores; (a–d) Type III; (e) Type IV; (f) Type V; all figures $\times 1,000$, except (f), $\times 500$. (a) Part of a sporangial mass showing spores with small curvatural spinae and distal conical structures, 45A, tilt 90° . (b) Detail of spores from another sporangium showing sculpture of grana and conical structures, 181A, tilt 0° . (c–d) Specimens showing larger distal sculpture borne by mural ridges or separated by lacunae, 169A, (c), (d) tilt 45° . (e) Specimen similar to Type III but with pronounced curvatural spinae, 45A, tilt 90° . (f) Sporangial mass of Type VA tetrads, 91A, tilt 90° , $\times 500$.

localities A-008100 and A-008104, upper *annulatus-sextantii* Assemblage Zone, late Emsian; (e) Sextant Formation, northern Ontario (McGregor & Camfield 1976); GSC localities A-007850 and A-007855, lower *douglastownense-euryptero* Assemblage Zone, late Emsian; (f) Malbaie Formation, Gaspé, Quebec (McGregor 1977); GSC localities A-007132 and A-007138, *velatus-langii* Assemblage Zone, early Eifelian; (g) McAdam Lake Formation, northern Nova Scotia (McGregor unpublished); GSC locality O-094437, lower *velatus-langii* Assemblage Zone, early Eifelian; (h) Williams Island Formation, northern Ontario (McGregor & Camfield 1976); GSC localities A-008057 and A-008058, *devonicus-naumovae* Assemblage Zone, early Givetian; (i) Cape De Bray Formation, Melville Island (McGregor, in press); GSC locality C-129628, *velatus-langii* Assemblage Zone, early Eifelian; (j) Bird Fjord Formation, Ellesmere Island (McGregor unpublished); GSC locality O-100909, *velatus-langii* Assemblage Zone, early Eifelian; (k) Bird Fjord Formation, Bathurst Island (McGregor unpublished); GSC locality O-100837, *velatus-langii* Assemblage Zone, early Eifelian; (l) Bird Fjord Formation, Devon Island (McGregor unpublished); GSC locality C-007678, lower *devonicus-naumovae* Assemblage Zone, mid-Eifelian; (m) Hecla Bay Formation, Ellesmere Island (McGregor unpublished); GSC locality C-091990, *velatus-langii* Assemblage Zone, early Eifelian; GSC locality C-091951, *devonicus-naumovae* Assemblage Zone, late Eifelian or early Givetian.

The ages assigned to these strata are based on their spore assemblages. For some of them, the age determinations have been supported by associated marine faunas, i.e. (d) conodonts (T. T. Uyeno, personal communication to DCM); (h) shelly faunas (Sanford & Norris 1975); and (j) conodonts (T. T. Uyeno, personal communication to DCM).

Specimens of *Acinosporites lindlarensis* from these localities were re-examined and classified into types and subtypes using the Blenheim-Gilboa spores for comparison. Table 1 shows the range of morphological variation of spores at each stratigraphic level (except levels with only rare specimens of uncertain assignment).

The following spore types and subtypes were either not seen or were rare at Blenheim-Gilboa:

Type I, Subtype ID (Fig. 14). The curvatural spinae are irregular, occasionally biform with bulbous bases (Fig. 14j). The spine bases are coarser than all other Type I spores, but in specimens 'cf. ID', some of the spinae are uniformly tapered. Distal sculpture consists of close-packed biform elements fused into groups (Fig. 14d). In some specimens the distal tuberculae are large and biform, in others the distal sculpture consists of 'beaded' ridges and irregular polygons similar to those of Subtypes IA and IB.

Type II (Fig. 15a, b, f). Curvatural spinae are small; biform elements are reduced and have faint interconnections. Type II from Blenheim-Gilboa exhibits a wide range of variation based on few specimens.

Subtype IIA (Fig. 15f). Curvatural spinae are evenly tapered, as Type I, and extended biform. The small distal biform sculptural elements are spaced with indistinct interconnections.

Subtype IIB. Stout biform elements occur on low ridges. Their bases may be crowded together with polygonal outlines.

Among the spores found in dispersed spore residues, specimens similar to subtypes IIA and IIB (Fig. 15 a-b) were found only in lower Eifelian sediments from Gaspé. They are listed as Type II in Table 1.

Type cf. V (Fig. 16e). Like Type V, but the distal sculpture is more widely spaced than typical Type V and some specimens bear discontinuous groups of elements.

Subtype VC (Fig. 17a-b). Like Type V from Blenheim-Gilboa, with biform elements fused into crowded, broad, sinuous ridges (acanthomammillate) but lacking curvatural spinae. Proximal sculpture consists of prominent biform units, appearing under the light microscope as scattered large grana, surrounded by discrete finely granulate elements, or with interconnections between biform units (seen only under SEM).

Subtype VD (Fig. 16a-d). Like VC but a few curvatural biform units show extended spinae. In contrast, Type V (Blenheim-Gilboa) has evenly tapered curvatural spinae, but these are rarely seen because the spores are in tetrads. In some specimens with biform curvatural spinae, the distal sculpture consists of biform elements with low broad bases so crowded together they form a polygonal pattern.

Type VI (see page 130). Small sculptured varieties found dispersed as separate spores are also referred to Type VI, but the *in situ* spores at Blenheim-Gilboa occur only in tetrads and precise comparisons are, therefore, not possible. Some dispersed specimens having more or less parallel-sided elements, and others with more rounded biform elements are referred to as ?Type VI (compare Figs. 17e and 13c).

Subtype VIA. No good curvatural spinae; distal sculpture small, beaded to crowded micro- and biform elements.

Subtype VIB. The curvatural spinae are slender. Distal sculpture varies from crowded to spaced.

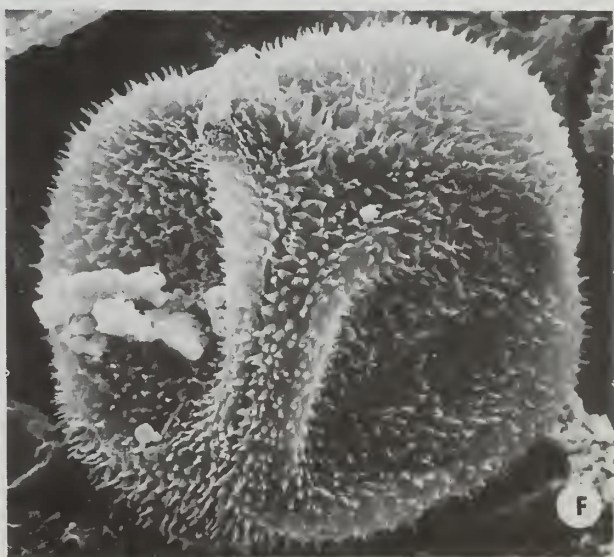
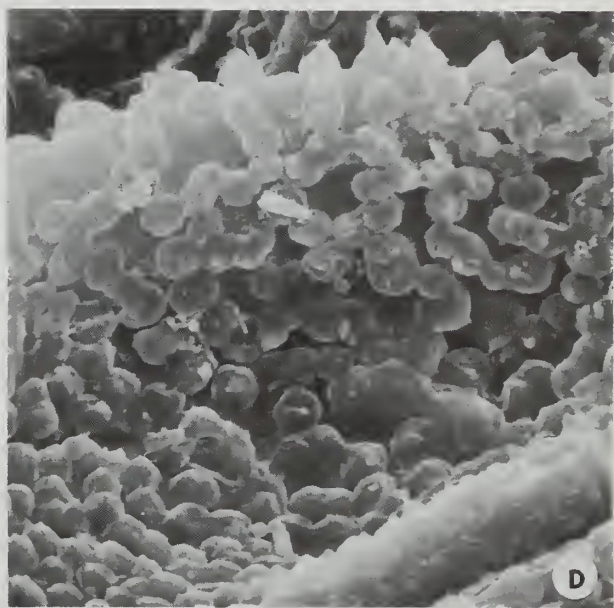
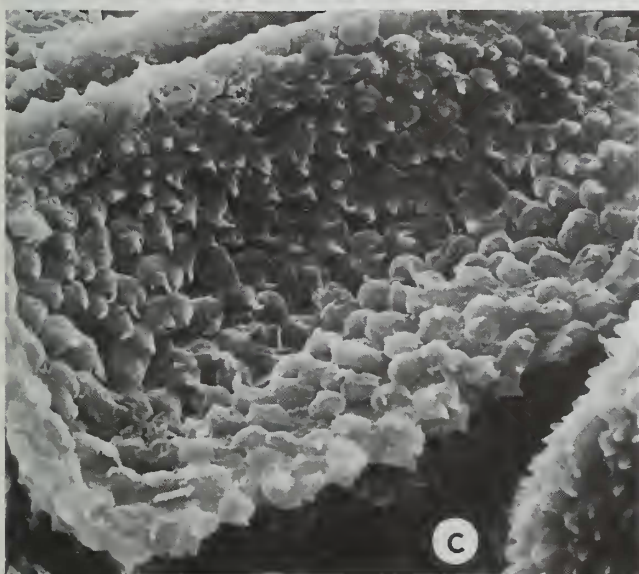
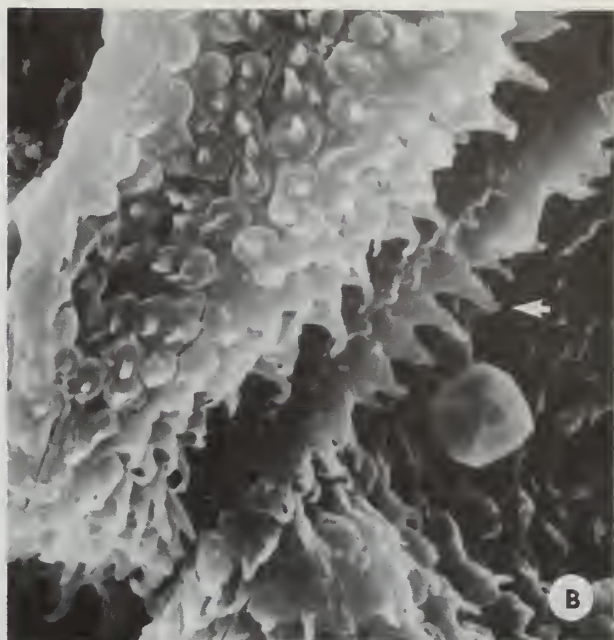
Subtype VIC. The curvatural spinae are a mixture of evenly tapered, biform and parallel-sided elements. Distal sculpture varies from crowded to spaced.

The spore data from the localities we have investigated have been plotted in stratigraphical sequence (Table 1). The table shows that for each successive palynodeme, the range of variation as expressed by the types and subtypes of *Acinosporites lindlarensis* is different. In the lower Givetian, Type I subtypes are dominant, whereas in the Emsian only subtypes of V and VI are present.

Examples in the literature

With few exceptions, the published records of *Acinosporites lindlarensis* are inadequately illustrated for detailed comparison and assignment to the informal types proposed herein. Nevertheless, the taxon is widely reported (see Appendix II) and specimens illustrated from the Emsian/Eifelian interval tend to have small, biform curvatural spinae (e.g. Riegel 1968, 1973) in contrast to the dominantly large spinae of the Givetian material.

Fig. 9 *Leclercqia complexa* from Blenheim-Gilboa, scanning electron photomicrographs of *in situ* spores; (a-d) Subtype VA, sporangium 91A; (e) Subtype VB; (f) cf. Type VI, sporangium 91B. (a) Tetrad, tilt 45°, × 1,200. (b) Detail of spore in (a) showing small, evenly tapered curvatural spinae (arrow) and biform distal elements, tilt 45°, × 3,000. (c) Detail of distal sculpture in (a) showing crowded biform elements, tilt 70°, × 2,000. (d) Detail of (a) showing beaded ridges over distal polar area, tilt 45°, × 3,000. (e-f) Tetrads: (e) biform distal sculpture small and crowded, tilt 45°, × 1,000; (f) smaller specimen showing more elongate distal spinae, tilt 45°, × 1,200.



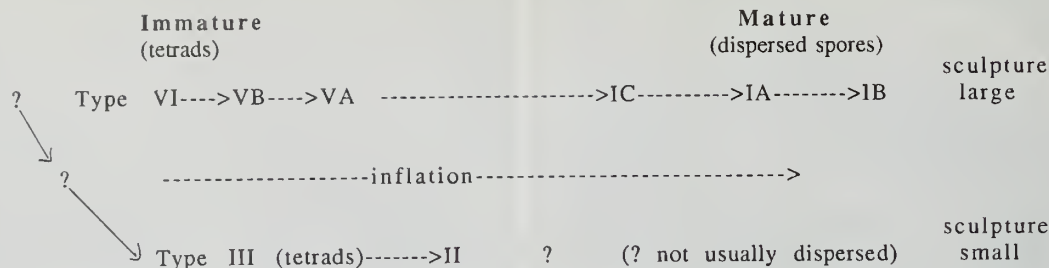


Fig. 10. Maturation sequence of spores found in *Leclercqia complexa*. Inflation refers to increase in spore size as a partial cause of changes in sculptural pattern.

PATTERN OF EVOLUTION OF THE *LECLERCQIA* LINEAGE

The data in Table 1 and Fig. 18 show changes in the number and variety of types and subtypes from the *annulatus-sextantii* Assemblage Zone of middle Emsian age to the upper part of the *devonicus-naumovae* Assemblage Zone of late Eifelian age. Emsian assemblages have spores of basically two kinds, Types V and VI (Fig. 19a). Subtypes of Type V occur *in situ* in *Leclercqia* sp. nov. (Kasper) and are closely similar to immature spores of Type V from Blenheim-Gilboa. Spores of Type VI are regarded as the most immature in our Blenheim-Gilboa maturation sequence, but are not seen *in situ* in the Dalhousie material, possibly because of the smaller amount of material examined. However, subtypes of Type VI reflect a second tendency, the 'parvulus' tendency, seen in dispersed material in which some varieties have small sculpture. Spores showing the 'parvulus' tendency are rare, only 3 of 132 specimens among Blenheim-Gilboa dispersed spores (see Table 1, Fig. 19b), but are more common (see e.g. Fig. 17e, f) among Emsian dispersed spores (26 specimens) where they are almost numerically equal to spores of Type V (23 specimens).

In lower Eifelian assemblages from Gaspé (Malbaie Formation) and Nova Scotia (McAdam Lake Formation), spores of *Acinosporites lindlarensis* tend to have small curvatural spinae, and in both regions a few specimens have some evenly tapered and pointed spinae (cf. I, cf. IC, Fig. 15c-e, g, h). The occurrence of specimens comparable with Type I in the Eifelian marks the appearance of a character that dominates later (Givetian) assemblages. Other specimens from the above named formations have curvatural spinae of Type I and small sculpture on low ridges (? Subtype IIA). Spores with small distal sculpture and curvatural spinae are dominant (Type II, ?II) in both areas, but the McAdam Lake Formation contains two specimens belonging to VD with crowded distal sculpture and biform curvatural spinae.

Thirteen specimens were recovered from six early Eifelian to early Givetian localities in the Canadian Arctic (Cape De Bray, Bird Fjord and Hecla Bay formations). Spores from both the *velatus-langii* and *devonicus-naumovae* zones

(Table 1) show two characteristic features: i) prominent curvatural spinae, some tending to be evenly tapered (cf. I, cf. IA) and others stout and biform (?ID, ID); and ii) small sculpture (Type VI).

Specimens from the early Givetian Williams Island Formation show morphographic variation like that of spores from Blenheim-Gilboa, with 46 out of 48 spores belonging to subtypes of Type I. The main differences from the New York specimens is that the majority of spores (41) are of Subtype ID, which possesses large biform curvatural spinae with bulbous bases. Some spores have crowded distal sculpture (IC, cf. IC) and others have evenly tapered spinae interspersed with biform ones. The two remaining spores belong to subtypes with small sculpture.

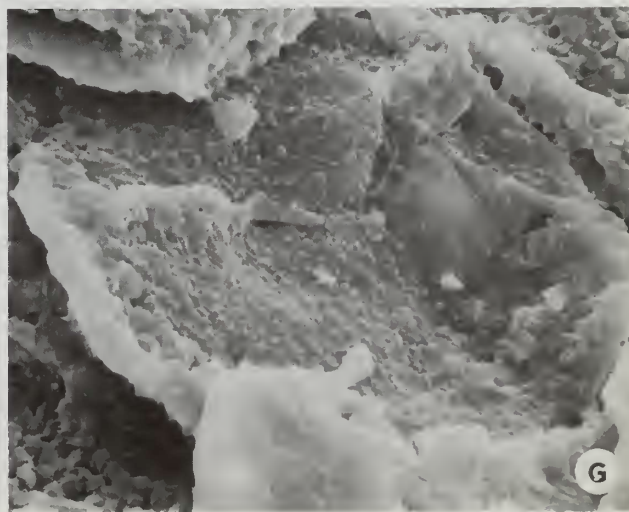
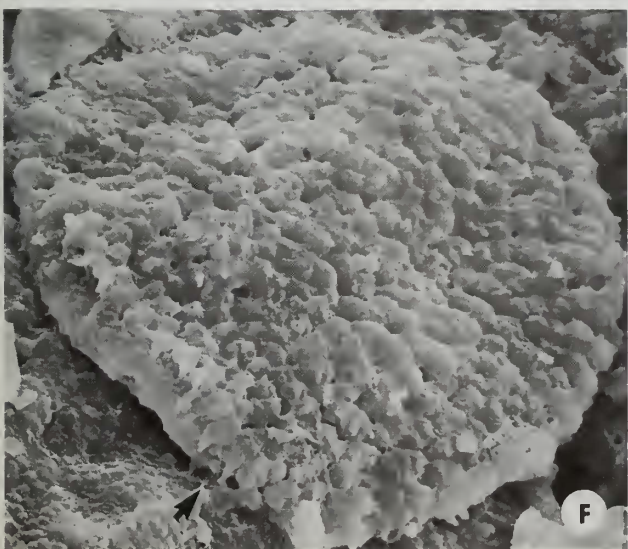
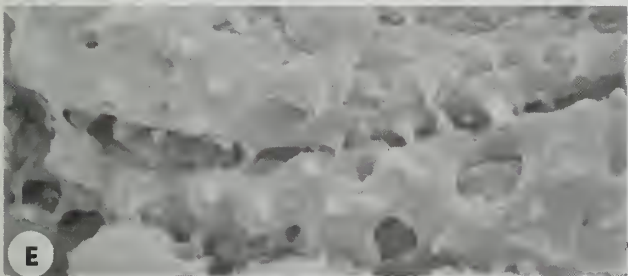
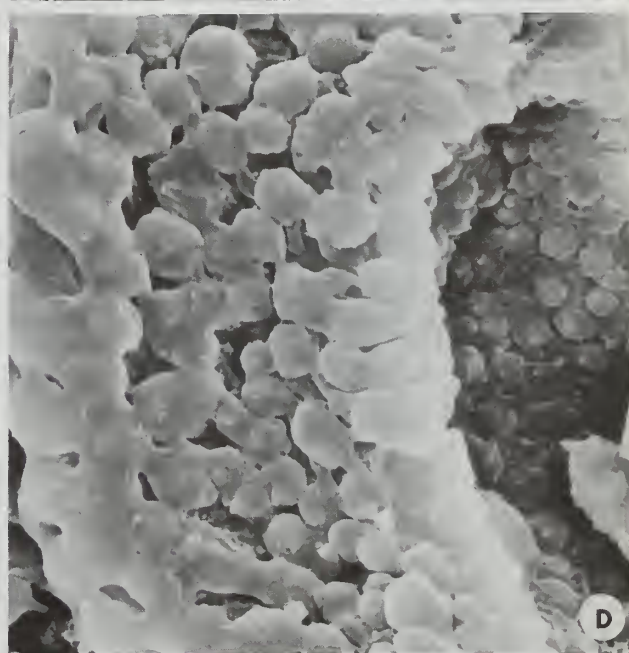
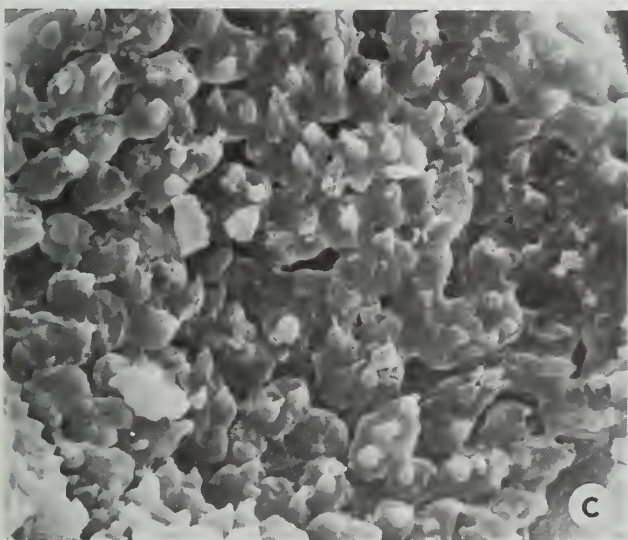
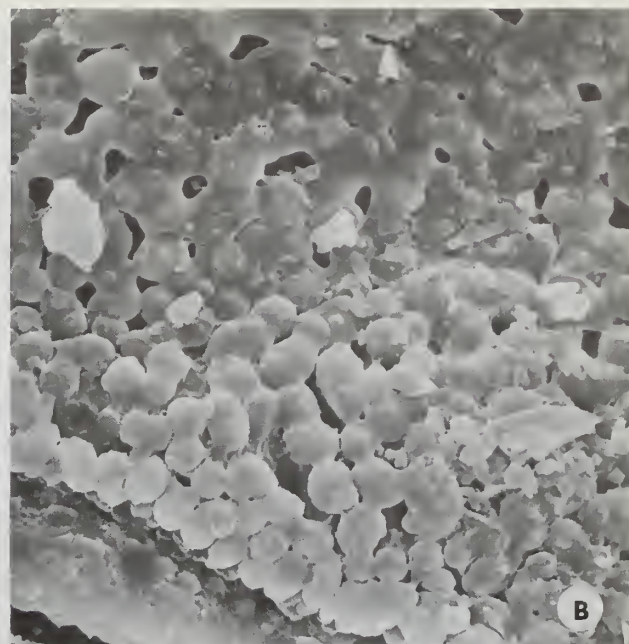
The succession of spore types shows an increasing tendency with time towards the development of large Type I (Fig. 18) curvatural spinae as seen in the material from Blenheim-Gilboa, with a secondary but persistent tendency to produce fewer dispersed spores with small sculpture.

COMPARISON WITH SPECIES OF DISPERSED SPORES OF SIMILAR SCULPTURE

In the Middle Devonian, a number of species first described from the Orcadian Basin of north-east Scotland (Richardson 1965), but subsequently reported from other regions, show some features in common with *Acinosporites lindlarensis*. These include spores with large sculptural elements, i.e. *A. acanthomammillatus* Richardson 1965, *A. macrospinosus* Richardson 1965, *Corystisporites multispinosus* Richardson 1965, and others with small sculpture, *A. parviornatus* Richardson 1965. *A. acanthomammillatus* shows a distal sculpture like that of Type V. In *A. macrospinosus* the spinose part of the biform unit is greatly extended forming large distal spinae superimposed on convolute ridges. The Scottish spores also have a larger size range than the spores in New York State.

Acinosporites is abundant in some strata in the lower part of the *devonicus-naumovae* Assemblage Zone. Here, in a

Fig. 11 *Leclercqia* sp. nov. from New Brunswick, Campbellton Formation, *douglastownense* — *eurypterota* Zone. Scanning electron photomicrographs of *in situ* spores of Type V; (a-e) Subtype VC; (f and g) Subtype VD. All figures tilt 45°, except Fig. e, tilt 90°. (a-b) Equatorial view showing foveolate distal polar area with conical and subequatorial area with murornate ridges, stub 257: (a) × 1,000; (b) detail of same spore, × 2,000. (c) Specimen showing biform elements superimposed on murornate ridges, stub 258, × 2,000. (d) Equatorial view showing curvatural elements with no spinose terminations, stub 267, × 3,000. (e) Detail of distal polar surface showing spinae and foveolate exine, stub 256, × 3,000. (f) Distal view showing small curvatural spinae (arrow), and crowded distal ridges, stub 257, × 1,000. (g) Proximal view showing relatively coarse sculpture over the contact areas and rupture of exoexine showing 'intexine' (arrow), stub 257, × 1,000.



part of the sequence dated as late Eifelian (based on spores), a third species of *Acinosporites*, *A. parviornatus*, is distinguished from the other two by its small, biform sculptural elements and ridges over the distal surface, an ornamentation similar to that in Type VI spores described herein. It lacks the curvatural spinae of some Type VI spores. *Corystisporites multispinosus* is also found in the Orcadian Basin. The distal ornament consists of biform spinae fused in groups. Such spores differ from *A. lindlarensis* in having lips elevated as an apical prominence, no visible wall separation and biform spinae all over the distal surface. The species is unlike any of the types and subtypes described, but reduction of the apical prominence and the distal biform spinae would produce a spore approaching Type I, with similarities to Subtypes IB and ID.

Thus, *Acinosporites* spp. in Scotland show morphographic features in common with certain types and subtypes of the *A. lindlarensis* morphon. Yet none of the species exactly match spores found *in situ*. Were such spores produced by other species of *Leclercqia*, or by plants of a related genus? The close similarity of some of the sculptural patterns, e.g. of *A. acanthomammillatus* and Type V suggests that their parent plants were related and perhaps diverged from a common ancestor in the Emsian. In this respect it is interesting to note that *Leclercqia* sp. nov. has spores that resemble in many ways *A. acanthomammillatus*, which first appears in the Lower Eifelian and perhaps represents the divergence of a separate *Leclercqia* species.

BIOLOGICAL IMPLICATIONS

The *in situ* spores from two species of *Leclercqia*, *L.* sp. nov. and *L. complexa*, show different ranges of sculptural variation. A comparison between the two complexes of *in situ* spores shows different combinations of types and subtypes (Fig. 19c, d). Additionally, dispersed spores contemporaneous with the *in situ* spores and from other beds of Emsian, Eifelian and Givetian age show a shifting pattern of types and subtypes (Fig. 18). Emsian strata contain types clustering around Kasper's *in situ* material, whereas Givetian spores show much more similarity to the *in situ* material from New York State. Thus both the macro- and microfossil evidence suggest evolutionary change from the Emsian to the Givetian. Further, the dispersed spore evidence from intervening stratigraphical levels (Eifelian to lower Givetian) shows that evolutionary change in the spores was gradual (Fig. 18, Table 1) and the pattern of types closely reflects the maturation sequence postulated for *L. complexa* (see Fig 10). The *in situ* spores of *Leclercqia* sp. nov. are closely similar to the tetrads (Type V) of *L. complexa* in the lower Givetian from New York State. Most of the dispersed spores associated with that plant are similar to Type V. Thus 'mature' spores from the Emsian most closely resemble 'immature' spores from the early Givetian (palingenesis), perhaps reinforcing the genetic relationship between *Leclercqia* sp. nov.

and *L. complexa*. *L. complexa* has also been described from the Givetian of Germany and Australia and the lower Givetian of Belgium (Fairon-Demaret 1974, 1980, 1981). Similar forms (*L.* cf. *complexa*) have been described from older strata (lower Eifelian of Belgium, Fairon-Demaret 1981). A few dispersed spores from the matrix of the Belgian material are illustrated by Fairon-Demaret (1981, Pl. 1, figs 7–10) and appear to belong to Type I.

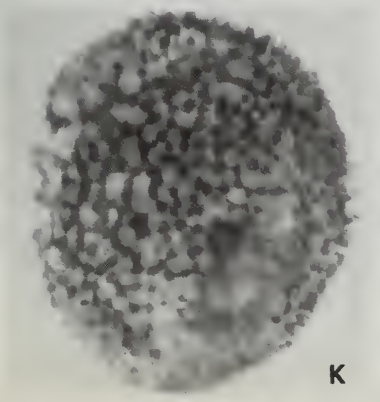
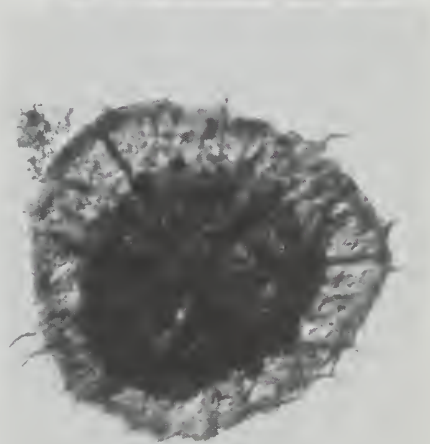
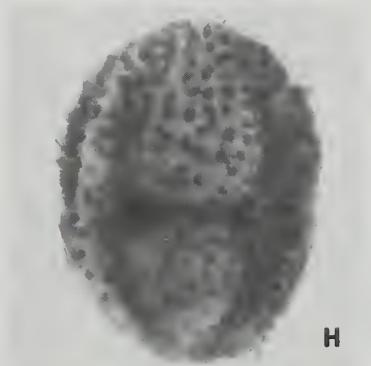
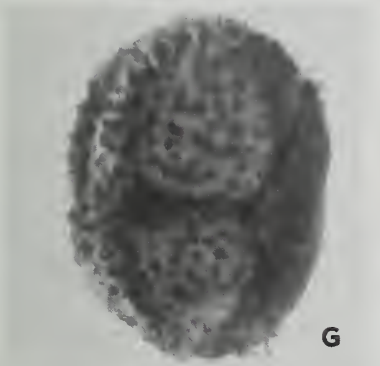
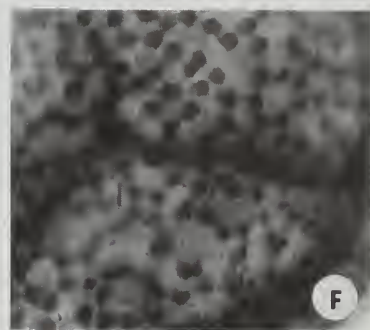
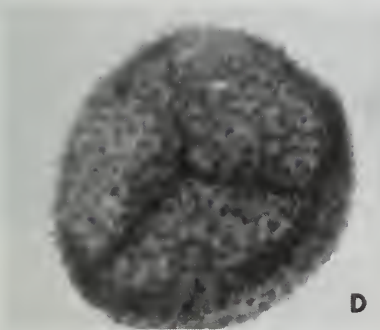
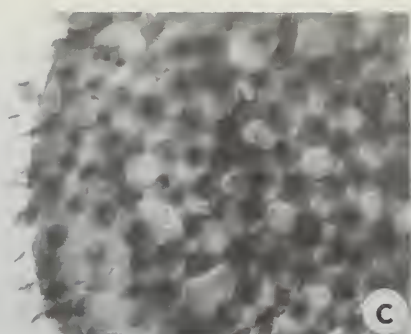
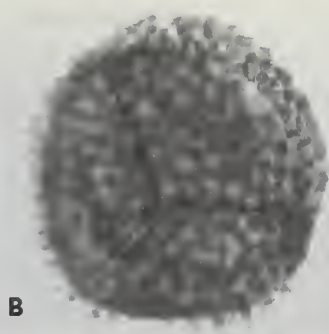
STRATIGRAPHICAL IMPLICATIONS

Within the morphon *Acinosporites lindlarensis* the component types and subtypes intergrade and within each stratigraphical interval the plexus of spores (palynodeme — 'palynodeme') is different. The stratigraphical range of *A. lindlarensis* (middle Emsian to lower Givetian) embraces nine palynodemes — 'palynodemes' (Table 1, excluding those of *Leclercqia complexa* and *L.* sp. nov. spores) and each is apparently unique, providing greater potential for stratigraphical refinement than the undivided taxon *A. lindlarensis*.

Evenly tapered curvatural spinae are rare and small in the Emsian and occur more abundantly in Eifelian rocks. Larger, typical Types IA, B, and C curvatural spinae are most common in Givetian strata. As the overall trend is towards increase in the prevalence of spores with such spinae, the Williams Island Formation with its predominance of specimens with biform curvatural spinae may be older than Blenheim-Gilboa sediments, where spores with large, evenly tapered curvatural spinae predominate. An alternative hypothesis is that this different variation in the two lower Givetian samples is due to geographical factors, but our data do not allow us to explore such a possibility further. Thus, the spores of the two *Leclercqia* species appear to have undergone palingenesis and gradualistic evolution between the late Emsian and early Givetian. The early stages of spore maturation in the Givetian sporangia repeat the morphology of mature spores in the upper Emsian. There is evidence for a lineage of spores from the Emsian to the Givetian. Emsian specimens have larger proximal sculpture, a partially foveolate distal exine, subequatorial closely packed ridges and small, sometimes biform curvatural spinae. In the mature spores of *L. complexa* from the Givetian, large, evenly tapered, curvatural spinae are dominant and biform spinae are rare. The distal ornament in dispersed spores throughout the Emsian-Givetian sequence is variable, showing a similar range of variation to that seen in the Blenheim-Gilboa material. For example, both beaded ridges and closely packed sculpture occur in earlier 'palynodemes'. Spores with barely discernible ridges connecting the biform elements occur throughout most of the sequence, and are most abundant in the Eifelian.

Type VI spores with small sculptural elements ('parvulus' tendency) are most abundant in the Emsian, where they may represent a natural variant. These spores are rare in dispersed

Fig. 12 Dispersed spores from Blenheim-Gilboa, specimens photographed using Nomarski differential interference contrast on a Zeiss Photomicroscope; (a–l) *Acinosporites lindlarensis*. All magnifications $\times 500$ except (c) and (f) $\times 1,000$, (m) and (n) $\times 250$. (a–c) Subtype IA, distal view, lacunose; (a–b) general view; two different focal levels. (c) detail of distal sculpture in plan. (d–f) Subtype IB, distal view, beaded ridges: (d–e) general view, two different focal levels; (f) detail of distal beaded ridges in plan. (g–h) cf. Subtype IB, distal view at two focal levels to show sculpture. (i–j) Subtype I. (k–l) Subtype I, distal view at two focal levels. (m) *Spinizonotrites* sp. cf. *S. naumovae* (Kedo) Richardson 1965. (n) *Calypiosporites* sp. cf. *Grandispora libyensis* Moreau-Benoit 1980.



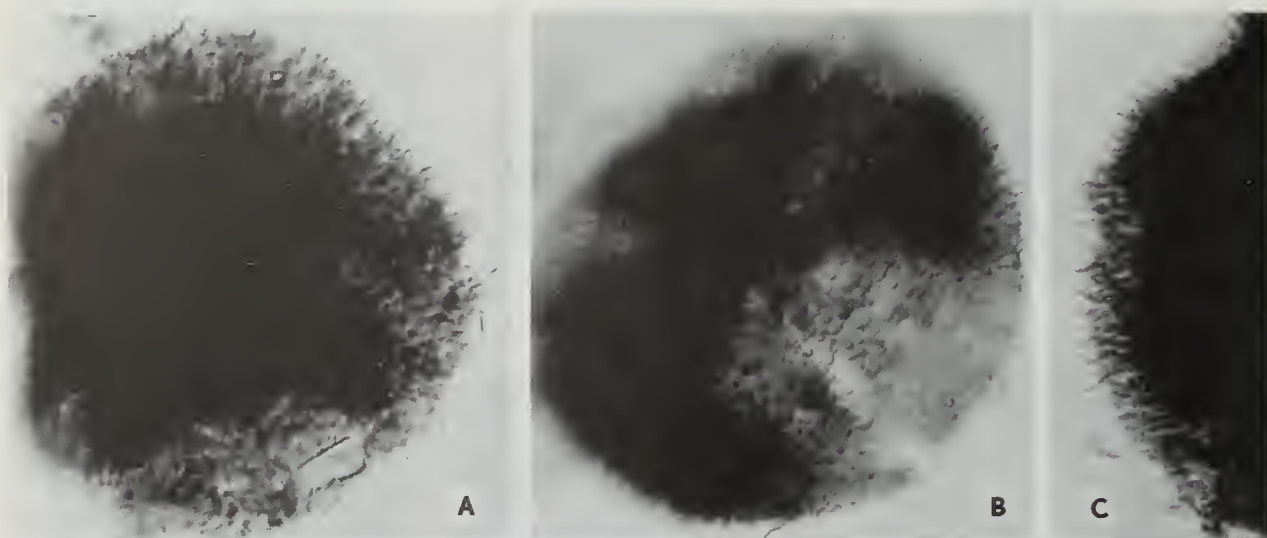


Fig. 13 *Leclercqia complexa* from Blenheim-Gilboa, light photomicrographs of *in situ* Subtype VI tetrads. (a) Tetrad showing sculpture of small biform elements. (b) Tetrad showing crowded bases of biform elements. (c) Detail of distal sculpture showing extended spinae on small biform elements.

assemblages at Blenheim-Gilboa, where they may represent an immature phase.

The dispersed spore record could now be checked for all of these features. Unfortunately, most publications showing this species contain photographs of only a few specimens so there is no indication of the range of variation at any particular horizon. Cramer (1969, pl. 2, fig. 27) illustrated a specimen that probably belongs to Subtype 1A/IB, from the Eifelian to ?lower Givetian *Gosseletia* Sandstone Formation of north-west Spain. Riegel's (1973, pl. 19, figs. 11–16) spores from the Eifelian of Germany show more crowded distal biform elements, resembling Kasper's Emsian spores and Type V. Like Kasper's material, that from the Rhineland has prominent proximal sculpture. *Geminospora treverica* from the late Emsian and early Eifelian (Riegel 1968) has some resemblance to specimens that are rare in Blenheim-Gilboa. Some specimens of *Acinosporites lindlarensis* (McGregor & Camfield 1976, pl. 5, figs. 2–3) have small curvatural spinae and more discrete distal biform elements, or elements fused in small groups (*ibid.*, fig. 5). Samples of Emsian and Eifelian age that contain abundant *A. lindlarensis* are needed so that the range of variation can be compared and the pattern of change in the lineage determined. Present indications are that taxonomic subdivisions of this lineage would be stratigraphically useful. Types V and VI could be used to subdivide the Emsian and Types I and II the Eifelian and lower Givetian. Knowledge of the range of variation seen in *Leclercqia* spores underlines the importance of describing the range of intraspecific variation in dispersed spore assemblages, from both the

evolutionary and the stratigraphical points of view.

SUMMARY AND CONCLUSIONS

Dispersed spore assemblages from middle Emsian to lower Givetian strata include a succession of intraspecific 'palynodemes' of *Acinosporites lindlarensis*. Each 'palynodeme' illustrates a range of variation that is unique in the sequences examined, and there is a morphological 'continuum' with the *in situ* spores of two species of *Leclercqia* of different ages. Mature dispersed spores of *Leclercqia* sp. nov. (Emsian) have a striking resemblance to presumed immature spores (Type V) of *L. complexa* (Givetian). Immature spores of *Leclercqia* sp. nov. are distally foveolate and have a subequatorial sculpture similar to that of *A. acanthomammillatus*. The pronounced similarity between the sculpture of Type V and its subtypes, and *A. acanthomammillatus* may also indicate close genetic affinity between the parent plant of *A. acanthomammillatus* and *L.* sp. nov. We can speculate, firstly, that the ancestors of *Leclercqia* sp. nov. may have borne foveolate spores with small distal coni and secondly, that in Eifelian time a related lycopod with spores of the species *A. acanthomammillatus* also existed.

Data in Table 1 may indicate either gradualism or punctuated equilibria, but when these data are grouped as in Fig. 18 they appear to indicate gradualism. We prefer gradualism

Fig. 14 *Acinosporites lindlarensis*, light photomicrographs of dispersed spores. All from Williams Island Formation, *devonicus* — *naumovae* Zone, except (f), Campbellton Formation, *annulatus* — *sextantii* Zone. All magnifications $\times 1,000$. (a–b) Typical Subtype ID, polar compression: (a) proximal view showing biform and evenly tapered curvatural spinae, small Y-folds and proximal sculpture; (b) distal view showing crowded, coarse, biform elements. (c) Subtype ID, equatorial view, fragment of a broken spore showing irregular, biform, slender spinae. (d–e) Subtype ID, distal view: (d) plan view of crowded, broad-based elements in rows interconnected by slender muri; (e) biform elements in profile with broad basal rounded 'tuberculae' terminated by slender coni. (f) Atypical specimen in proximal polar view, showing large, broad, short, curvatural elements similar to VC and distal sculpture of crowded small elements similar to Type VI (parvulus tendency). (g–i) Subtype ID, distal polar view: specimen with small, crowded acanthomammillate distal sculpture at three focal levels showing: (g) small biform sculpture; (h) thin intexine; (i) biform curvatural spinae. (j) Subtype ID, proximal polar view, showing large typical biform, broad-based curvatural spinae.

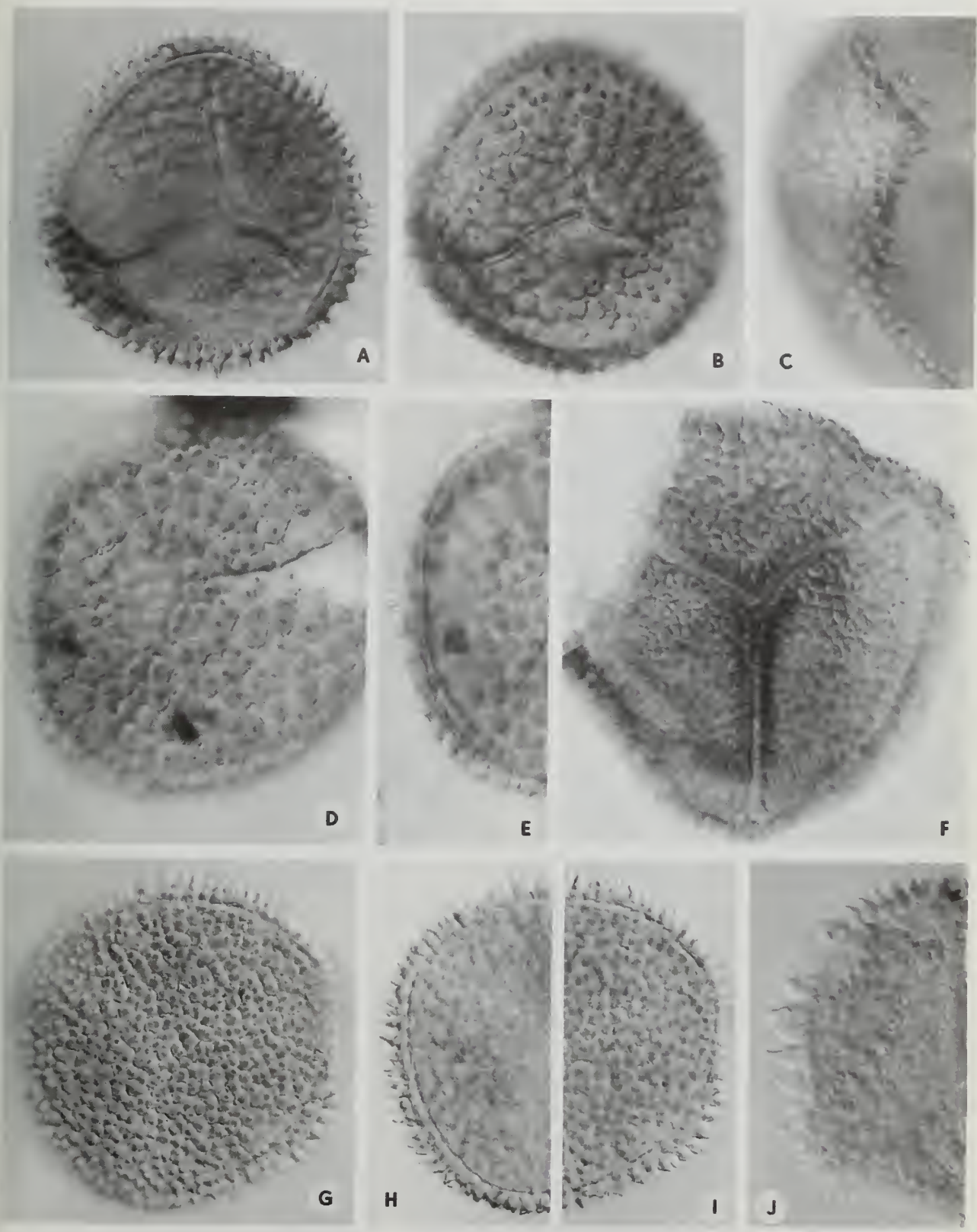
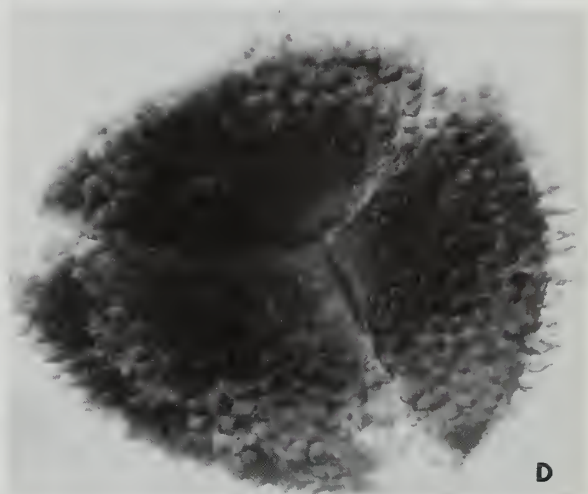
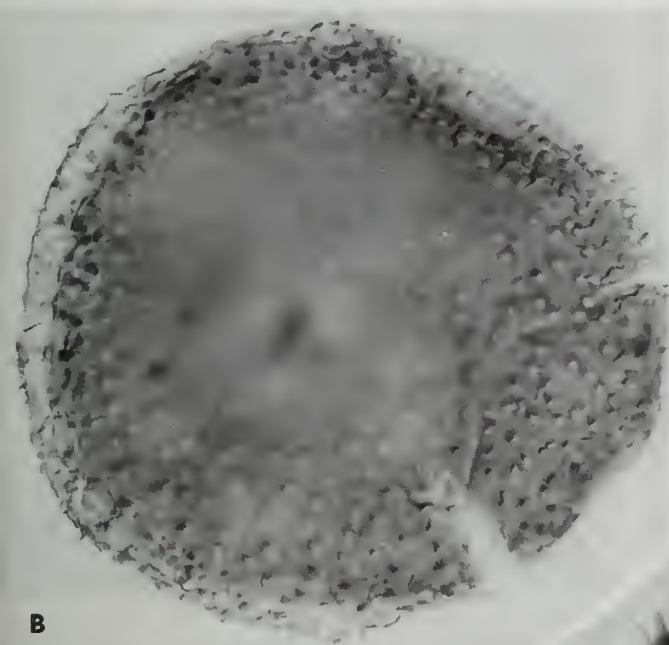
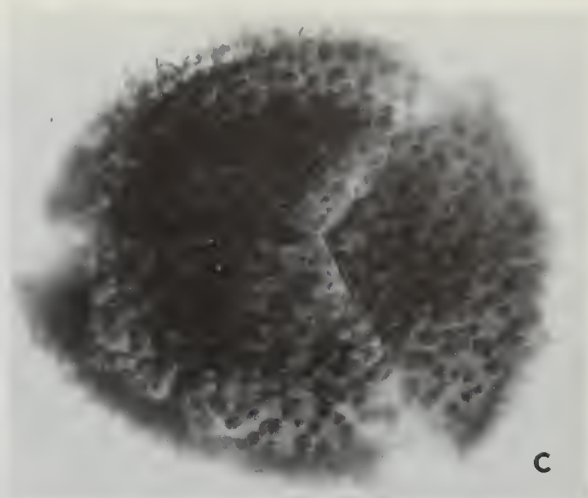
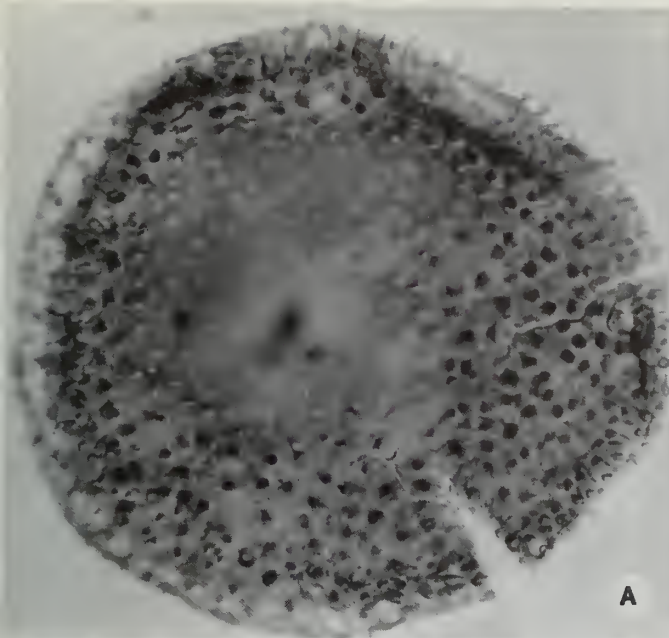


Table 1 *Acinosporites lindlarensis* types and subtypes: pattern of variation in 'Palynodemes' of different stratigraphical ages from Canada and New York State.

I	IA	IA/B	IB	IC	IA/C	ID	II	III	*V	*VC	VD	VI	VIA	VIB	VIC	TOTAL
Panther Mountain Fm., (upper <i>devonicus</i> — <i>naumovae</i> Zone), lower Givetian, Blenheim — Gilboa.																
	3?							2?				2?				
	lcf		lcf													
12	61	10	31	4	2		1	2				1				133
Panther Mountain Fm., (upper <i>devonicus</i> — <i>naumovae</i> Zone), lower Givetian, <i>Leclercqia complexa</i> in situ, Blenheim — Gilboa.																
29	142	1	7	4?	10		9	8				1?				
				55								27				293
Williams Island Fm., (<i>devonicus</i> — <i>naumovae</i> Zone), lower Givetian, Hudson Bay Lowlands.																
lcf	lcf			2cf		5cf								lcf		
				1		36							1			48
Cape De Bray, Bird Fiord and Hecla Bay Fms., (<i>velatus</i> — <i>langii</i> and <i>devonicus</i> — <i>naumovae</i> zones), lower Eifelian — lower Givetian, Canadian Arctic Islands.																
						2?				1?						
2cf	lcf					lcf										
						1						3		2		13
Malbaie Fm., (<i>velatus</i> — <i>langii</i> Zone), lower Eifelian, Gaspé.																
						9?										
lcf			3cf			lcf										
						6										20
McAdam Lake Fm., (<i>velatus</i> — <i>langii</i> Zone), lower Eifelian, Nova Scotia.																
						2?										
lcf											2					5
Sextant Fm., (<i>douglstownense</i> — <i>euryptero</i> Zone), upper Emsian, Hudson Bay Lowlands.																
										1?	1?	1?	1?			
						2cf							lcf	lcf		
										3	1		4	3		19
Campbellton Fm., (upper <i>annulatus</i> — <i>sextantii</i> and lower <i>douglstownense</i> — <i>euryptero</i> zones), upper Emsian, New Brunswick.																
						2?					1?					
						lcf										
						1	4	12	2		1					24
Campbellton Fm., (<i>douglstownense</i> — <i>euryptero</i> Zone), upper Emsian, <i>Leclercqia</i> sp. nov. in situ, New Brunswick.																
										2?	2?					
						2				80	57					143
Battery Point Fm., (upper <i>annulatus</i> — <i>sextantii</i> and lower <i>douglstownense</i> — <i>euryptero</i> zones), upper Emsian, Gaspé.																
												1		3	1	5
Stooping River Fm., (<i>annulatus</i> — <i>sextantii</i> Zone), middle Emsian, Hudson Bay Lowlands.																
												3?			2?	
										1	1	1			1	9

* Type IV, and Subtypes VA and VB, were seen in SEMs of *in situ* material from Blenheim-Gilboa. No attempt was made to count SEM material, but these types and subtypes were rare. In the count of the light microscope slides of the Panther Mountain Formation, only a single specimen, possibly assignable to Type IV, was seen.

Fig. 15 *Acinosporites lindlarensis*, light photomicrographs of dispersed spores, Malbaie Formation, *velatus-langii* Zone. All magnifications $\times 1,000$. (a-b) Subtype II?B, distal polar view: (a) low sculptural elements and basal 'tuberculae' only slightly elevated; (b) thin intexine almost equivalent in thickness to the exoexine. (c-e) Subtype cf. IC: (c) distal polar view with biform sculpture crowded except toward the equator; (d) median focus with curvatural spinae and polygonal distal spine bases; (e) part of the spore with curvatural spinae. (f) Subtype IIA, proximal polar view, specimen with subtriangular amb showing prominent Y-folds, small, distal, biform elements and small, slender Type I curvatural spinae. (g-h) Subtype cf. IC, broken, slightly tipped specimen: (g) variable proximal sculpture and stout curvatural spinae; (h) crowded, stout, distal, biform elements.



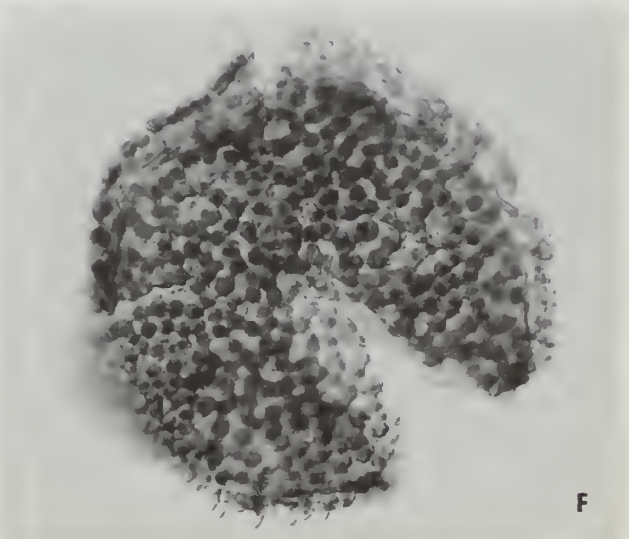
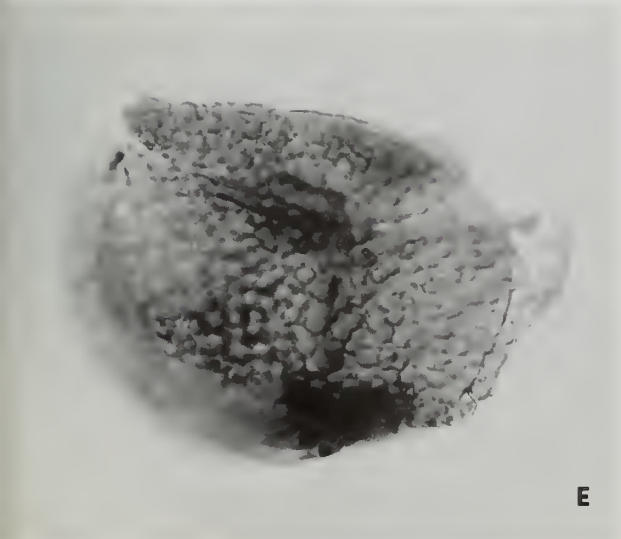
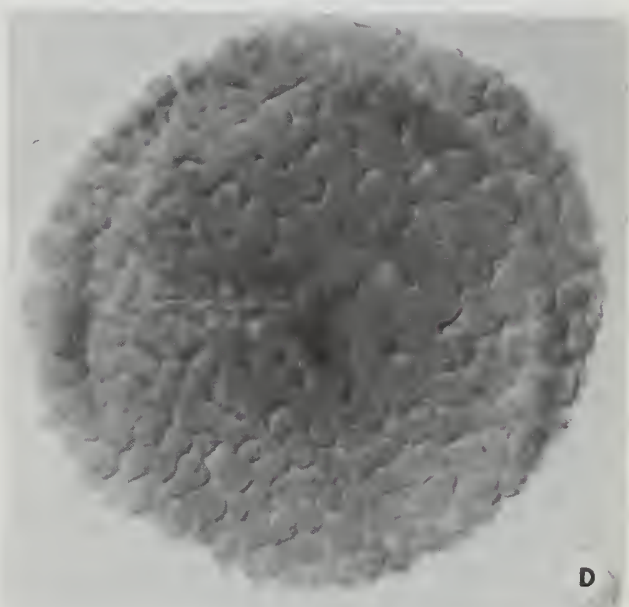
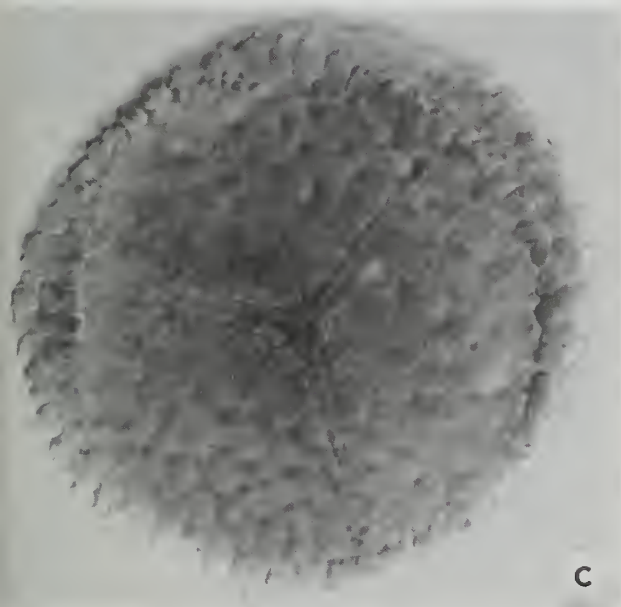
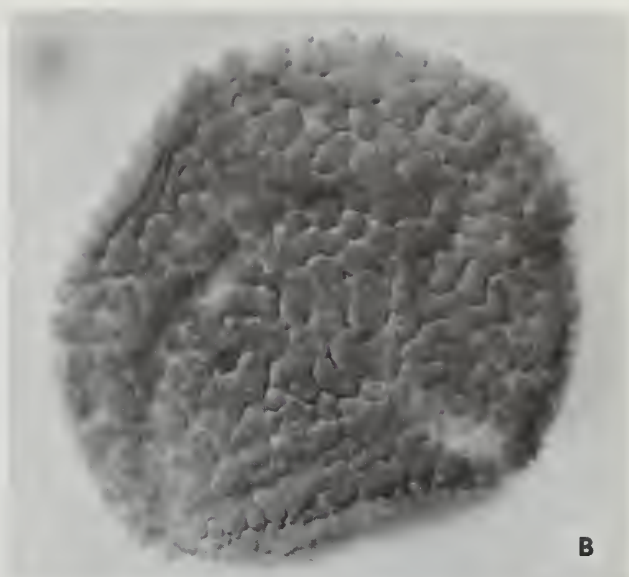
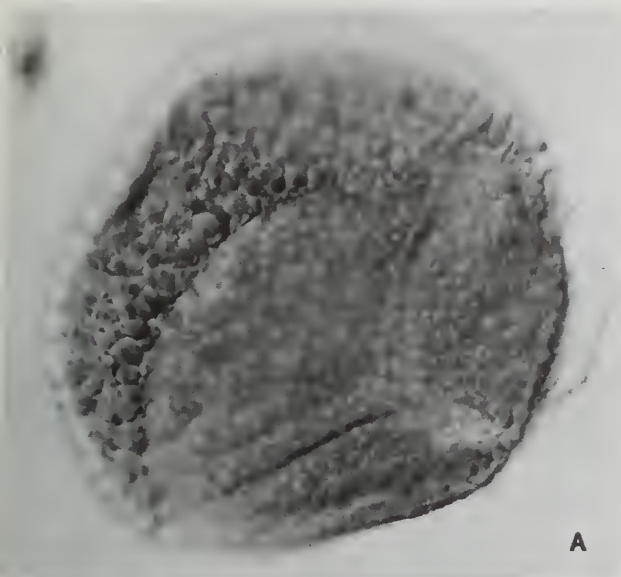
because the mature *Leclercqia* sp. nov. spores are closely similar to the immature spores of *L. complexa*. Furthermore, the morphographic ranges of types and subtypes overlap within the temporal sequence. The contemporaneous dispersed and *in situ* spores reflect the two plant species and the palynodemes — 'palynodemes' show progressively shifting sculptural modes with geological time. This is shown in Table 1: Emsian palynodemes — 'palynodemes' are dominated first by spores of Type VI ('parvulus' tendency) and later by Type V, whereas Eifelian and Givetian palynodemes — 'palynodemes' consist largely of subtypes of I and II, with subtypes of I increasing in abundance in younger strata. There is thus a need for further data from other localities to test, modify and amplify the succession suggested here.

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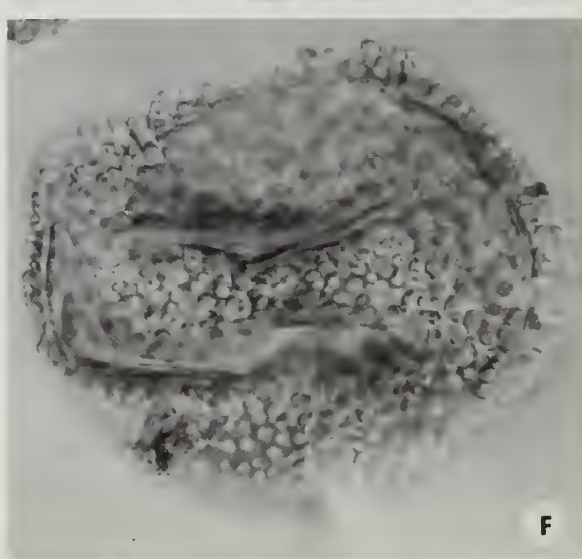
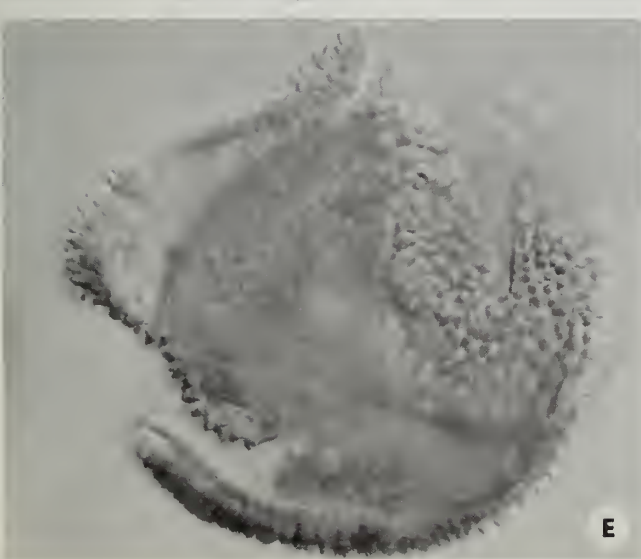
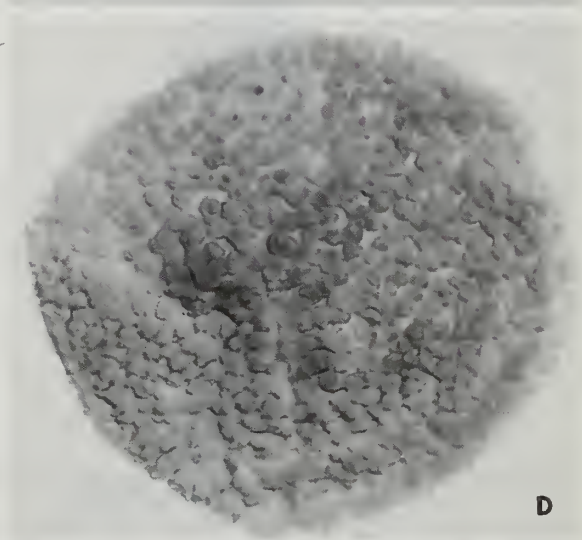
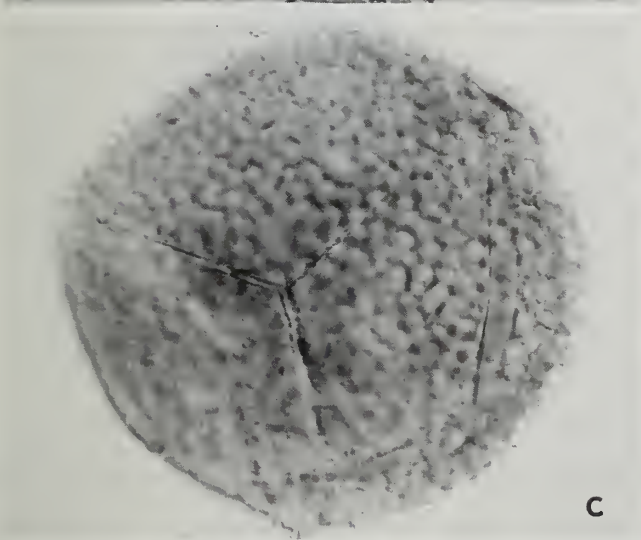
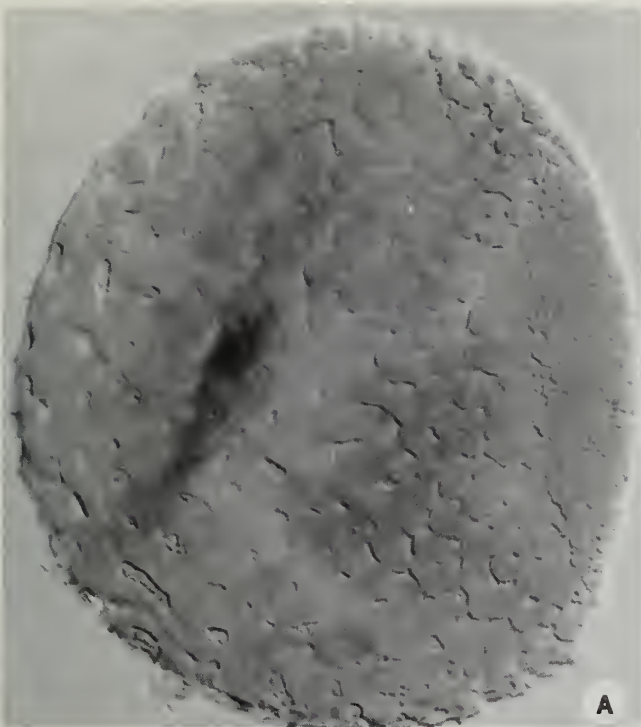
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Fig. 16 *Leclercqia* sp. nov. *in situ* spores (a-d) and *Acinosporites lindlarensis* dispersed spores (e-f), light photomicrographs; Campbellton Formation, *douglstownense-eurypterota* Zone. All magnifications $\times 1,000$. (a-b) Subtype VD, tipped specimen: (a) proximal view with biform 'tuberculae' and coarse proximal sculpture; (b) distal focus showing acanthomammillate sculpture and narrow canaliculae. (c-d) Subtype VD, proximal polar view: (c) proximal focus showing low lips and curvatural sculptural elements some of which have extended spinose terminations; (d) distal focus showing acanthomammillate to foveolate distal sculpture. (e-f) Subtype cf. V, matrix surrounding *Leclercqia* sp. nov.: (e) tipped specimen with split exoexine, laevigate 'intexine' and crowded, small sculpture; (f) distal polar view showing small sculpture like Type VI but forming a polygonal pattern like IA-B.



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Fig. 17 *Leclercqia* sp. nov. *in situ* spores (a–b) and *Acinosporites lindlarensis* dispersed spores (c–f); (a–d) Campbellton Formation douglstownense-eurypteroia Zone; (e–f) Stopping River Formation, *annulatus-sextantii* Zone, light photomicrographs. All magnifications $\times 1,000$. (a) Subtype VC, lateral compression showing foveolate distal area with slender conic, merging into typical acanthomammillate sculpture in the subequatorial region, no differentiation of curvatural sculpture and small proximal sculpture. (b) Subtype VC, distal polar view showing small biform elements and broad sinuous ridges. (c–d) Subtype VD–VI, matrix of *Leclercqia* sp. nov. Specimen with smaller sculpture than typical type VD spores: (c) proximal focus showing simple trilete sutures; (d) distal focus showing acanthomammillate sculpture. (e) ?Type VI, broken specimen with crowded, small, biform elements. (f) ?Subtype VD, broken specimen showing irregular curvatural spinae.



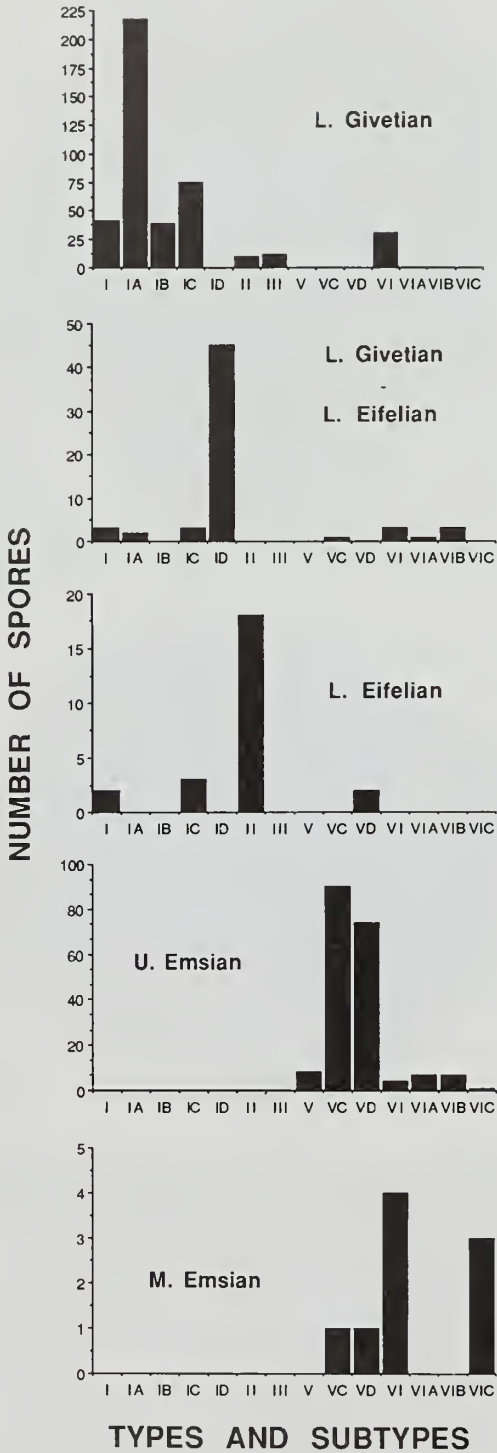


Fig. 18 Types and subtypes grouped into palynodemes — 'palynodemes' for five stratigraphical intervals, based on data in Table 1. Note that different vertical scales are used.

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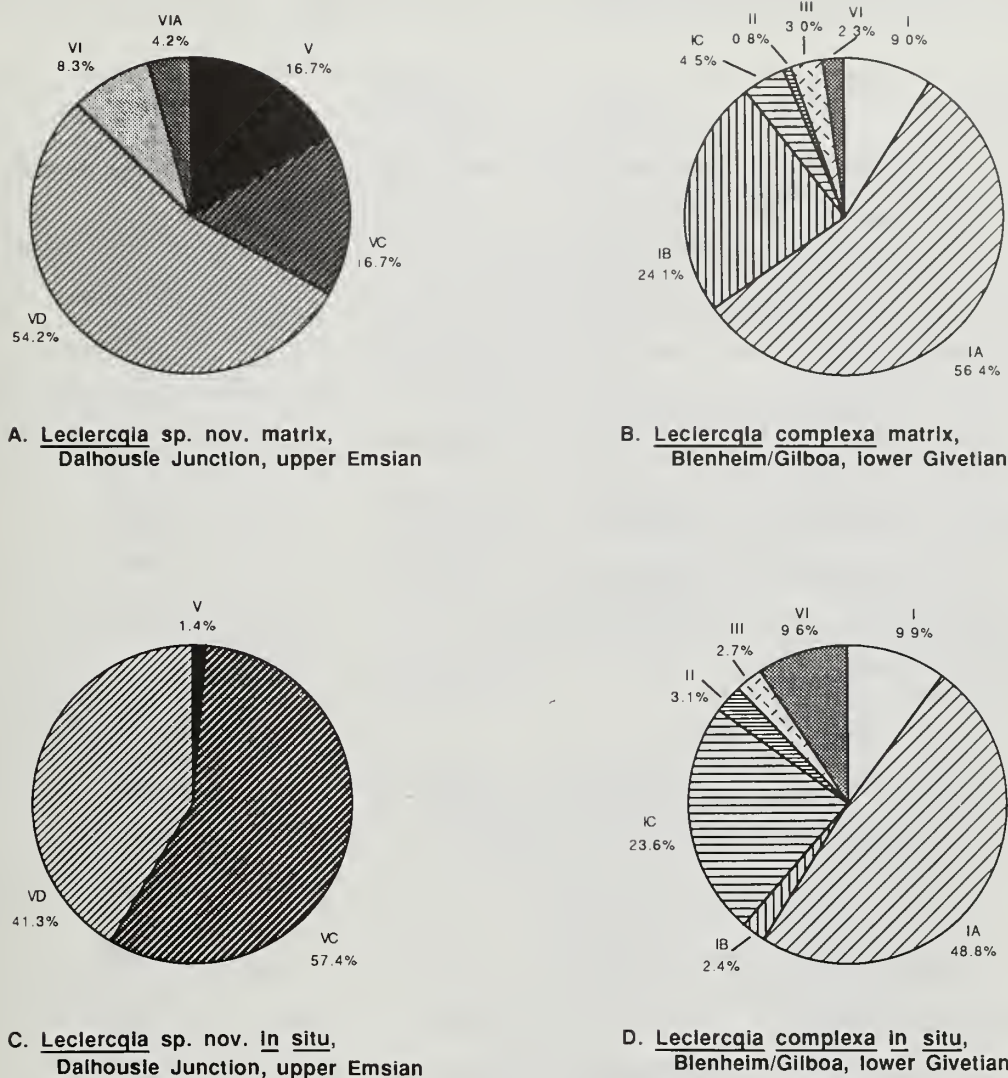


Fig. 19 Comparison between dispersed and *in situ* assemblages of spore types and subtypes from Dalhousie Junction and Blenheim-Gilboa.

APPENDIX I: REGISTER OF LOCALITIES

Locality no.	Locality	Formation	Location on Fig. 1
None	New York State, Schoharie County, along Schoharie Creek, cliff in west flank of Brown Mountain adjacent to electrical generating plant.	Panther Mountain	1
None	New York State, Schoharie County, Blenheim-Gilboa borehole B1, 1143.8 m N60E of reservoir near power plant.	Panther Mountain	1
GSC A-005368	Eastern Quebec, south shore of Gaspé Bay, 47 m north of small stream about 1.6 km northwest of Cap Rouge.	Battery Point	3
A-007102	Eastern Quebec, south shore of Gaspé Bay, 385 m north of Bois Brulé Brook.	Battery Point	3
A-007115	Eastern Quebec, south shore of Gaspé Bay, 732 m south of second stream south of Bois Brulé Brook.	Battery Point	3
A-007132	Eastern Quebec, south shore of Gaspé Bay, 59.5 m southeast of conglomerate of Pointe Jaune.	Malbaie	3
A-007138	Eastern Quebec, south shore of Gaspé Bay, 482 m southeast of first stream south of Pointe Jaune.	Malbaie	3
A-007850	Northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41'30"N, 80°48'00"W, 41.7 m depth.	Sextant	5
A-008057	Northern Ontario, Moose River Basin, Ontario Department of Mines Jaab Lake No. 1 well, 51°11'54"N, 82°56'00"W, 48.0-48.6 m depth.	Williams Island	6
A-008058	As above, but 51.7-52.3 m depth.	Williams Island	6
A-008100	As above, but 191.2-191.8 m depth.	Stooping River	6
A-008104	As above, but 204.6-205.2 m depth.	Stooping River	6
A-008785	Northern Ontario, Moose River Basin, Argor ETA No. 2 well, Kiasko River, 50°41'30"N, 80°48'00"W, 46.3-46.4 m depth.	Sextant	5
C-007678	Sheills Peninsula, Devon Island, 76°16'30"N, 95°15'00"W, 1.1 km from mouth of unnamed creek at Inglis Bay.	Bird Fiord	9
C-091951	Southwestern Ellesmere Island, western margin of inner Goose Fjord, 76°52'52"N, 88°43'01"W.	Hecla Bay	10
C-091990	Southwestern Ellesmere Island, river ca. 23 km south-southwest of Sor Fjord, 77°04'49"N, 84°34'17"W.	Hecla Bay	12
C-129628	Northeastern Melville Island, 75°52'N, 106°18'W, ca. 12 km east of Weatherall Bay	Cape De Bray	7
O-094437	Northern Nova Scotia, Cape Breton Island, 46°01'30"N, 60°24'40"W, roadcut 0.56 km northwest of McAdam Lake.	McAdam Lake	4
O-095530	Northern New Brunswick, south side of lower Restigouche River, 760 paces west of first access road to beach west of Dalhousie Junction.	Campbellton	2
O-096376	Northern New Brunswick, south side of lower Restigouche River, 48°02'30"N, 66°30'40"W, 0.8 km west of Dalhousie Junction.	Campbellton	2
O-096385	As above but 0.8 km west of Dalhousie Junction, about 0.6 m above high tide.	Campbellton	2
O-098401	Northern New Brunswick, south side of lower Restigouche River, 48°02'30"N, 66°30'40"W, 1200 m west of Dalhousie Junction.	Campbellton	2
O-098402	As above, but 1245 m west of Dalhousie Junction.	Campbellton	2
O-098403	As above, but 1072 m west of Dalhousie Junction.	Campbellton	2
O-098404	As above, but 925 m west of Dalhousie Junction.	Campbellton	2
O-100837	Bathurst Island, south of Dundee Bight, 75°50'00"N, 100°10'00"W, 226.0 m above base of section.	Bird Fiord	8
O-100909	Southwestern Ellesmere Island, north of Bird Fjord, 77°12'30"N, 87°02'00"W.	Bird Fjord	11

GSC = Geological Survey of Canada; Last column refers to numbers on Fig. 1.

APPENDIX II: Publications containing reference to *Acinosporites lindlarensis*

Author(s)	Date	Illustrations	Designation in Publication	Geographic Location	Designated age	Comment
Arkhangel'skaya	1976		<i>Geminospora treverica</i>	European USSR	Early Eifelian	
Arkhangel'skaya	1985a		<i>G. treverica</i>	European USSR	Late Emsian	
Arkhangel'skaya	1985b	Pl. 5, fig. 9,10	<i>G. treverica</i>	European USSR	Late Emsian to early Givetian	
Bär & Riegel	1974		<i>G. treverica</i>	Ghana	Givetian	
Brice et al.	1979		<i>Aneurospora</i> cf. <i>heterotunda</i> (sic)	France	Early Givetian	Assumed to be var. <i>lindlarensis</i>
Burjack et al.	1987	Pl. 1, Fig. 2	(var.) <i>lindlarensis</i>	Brazil	Late Eifelian to late Givetian	
Cramer	1969	Pl. 2 fig. 27	'Indeterminate'	Spain	Late Eifelian to Givetian	Probably var. <i>lindlarensis</i>
Edalat	1974		<i>lindlarensis</i>	Rhineland	Late Emsian	
Grey	1991	Pl. 1, fig. 9	<i>Dibolisporites</i> sp. cf. <i>echinaceus</i>	W. Australia	Late Givetian	Probably var. <i>lindlarensis</i>
Grey	1992	Pl. 1, figs. 6–8	<i>lindlarensis</i> ?	W. Australia	Late Givetian	Illustrated specimens not <i>lindlarensis</i> ?
		Pl. 14, figs. 1–4	<i>Dibolisporites</i> sp. cf. <i>D. echinaceus</i>	W. Australia	Late Givetian	Probably var. <i>lindlarensis</i>
Le Hérissé	1983	Pl. 4, figs. 9a–b, 10; Text–fig. 16	var. <i>minor</i>	France	Late Siegenian	
Lesuisse et al.	1979	Pl. 5, fig. 15	var. <i>minor</i>	Belgium	Late Emsian	
Lipatova	1984	Pl. 2, fig. 13	<i>G. treverica</i>	Siberia	Recycled	? Misidentified
Loboziak & Streel	1989	Pl. 2, figs. 5,6	(var.) <i>lindlarensis</i>	Tunisia, Libya	Late Emsian to early Frasnian	
Loboziak, Streel & Weddige	1990		<i>lindlarensis</i>	Germany	Early Givetian	
Marshall & Allen	1982	Pl. 30, figs. 2,5	var. <i>minor</i>	Shetland	Givetian	
Massa & Moreau-Benoit	1976	Pl. 3, fig. 3	<i>G. treverica</i>	Libya	Late Emsian and early Eifelian	
McGregor	1973	Pl. 6, figs. 17–21	(var.) <i>lindlarensis</i>	Gaspé (Canada)	Late Emsian and Eifelian	Also McGregor 1977
McGregor	1979a	Pl. 1, fig. 19	var. <i>lindlarensis</i>	Ontario (Canada) + unspecified	Late Emsian to early Givetian	
McGregor	1979b		(var.) <i>lindlarensis</i>	Unspecified	Late Emsian to early Givetian	
McGregor	1984	Pl. 2, fig. 21	var. <i>lindlarensis</i>	Bolivia	Late Emsian and early Eifelian	Identification questioned
McGregor & Camfield	1976	Pl. 5, figs. 2,3	var. <i>lindlarensis</i>	Ontario (Canada)	Late Emsian to Givetian	
		Pl. 5, figs. 4,5	var. <i>minor</i>	Ontario (Canada)	Late Emsian to Givetian	
McGregor & Camfield	1982	Pl. 1, figs. 9,10; Text–fig. 10	var. <i>lindlarensis</i>	Canadian Arctic Is.	Early Eifelian to early Givetian	
McGregor & Playford	1992	Pl. 1, fig. 1	var. <i>lindlarensis</i>	Eastern Canada	Late Emsian to late Givetian	
		Pl. 1, fig. 2	var. <i>lindlarensis</i>	Australia	Givetian	
		Pl. 1, fig. 9	var. <i>minor</i>	Ontario (Canada)	Late Emsian to late Givetian	
		Pl. 1, fig. 10	var. <i>minor</i>	W Australia	Early Frasnian	
McGregor & Uyeno	1972		(var.) <i>lindlarensis</i>	Canadian Arctic Is.	Eifelian and early Givetian	

Moreau-Benoit	1980		<i>G. treverica</i>	Libya	Late Emsian and Eifelian	
		Pl. 13, fig. 6	<i>G. libyensis</i>	Libya	Early and late Givetian	? var. <i>lindlarensis</i>
Moreau-Benoit	1989	Pl. 1, fig. 7	var. <i>lindlarensis</i>	Libya	Late Eifelian	Illustrated specimen misidentified ?
Moreau-Benoit & Massa	1988		<i>G. treverica</i>	Libya	Late Emsian	
Perez-Leyton	1990		<i>lindlarensis</i>	Bolivia	Late Eifelian, late Givetian and early Frasnian	
Ravn & Benson	1988	Pl. 5, figs. 1-3	var. <i>lindlarensis</i>	Georgia (USA)	Late Emsian and Eifelian	
Richardson	1974		<i>lindlarensis</i>	Canada, Belgium, Germany	Late Emsian to early Givetian	
Richardson & McGregor	1986	Pl. 6, fig. 8	var. <i>lindlarensis</i>	various	Late Emsian to early Givetian	
Riegel	1968	Pl. 19, figs. 11-16	(var.) <i>lindlarensis</i>	Rhineland	Mid Eifelian	Incl. holotype
Riegel	1973	Pl. 16, figs. 5-7	<i>G. treverica</i>	Rhineland	Late Emsian and early Eifelian	Incl. holotype
Riegel	1974		(var.) <i>lindlarensis</i>	Rhineland	Early to mid Eifelian	
			<i>Acinosporites treverica</i>	Rhineland	Early Eifelian	
Riegel	1982		(var.) <i>lindlarensis</i>	Rhineland	Late Emsian to early Givetian	
Schweitzer	1983	Pl. 2, fig. 7	(var.) <i>lindlarensis</i>	Rhineland	Early Eifelian	holotype
Stee mans	1989	Pl. 18, figs. 7-9, Text-fig. 35	<i>lindlarensis</i>	Belgium, Germany, Romania	Late Gedinnian to late Siegenian	Varieties not distinguishable
Stee mans & Gerrienne	1984		<i>lindlarensis</i>	Belgium	Late Gedinnian	Varieties not distinguishable
Stree l	1972	Pl. 2, figs. 1-7	<i>Aneurospora</i> cf. <i>heterodonta</i>	New York State (USA)	Late Givetian	'Associated with <i>Leclercqia complexa</i> '
Turnau	1985		<i>lindlarensis</i>	Poland	Late Emsian or early Eifelian	
Turnau	1986	Pl. 7, figs. 9, 12, 13	(var.) <i>lindlarensis</i>	Poland	Late Emsian or early Eifelian	
Vaitekunene	1983		<i>lindlarensis</i>	Lithuania	Late Eifelian	
Van der Zwan	1980	Pl. 1 fig. 9; Pl. 2, figs. 1,2	var. <i>minor</i>	Ireland	Late Emsian	

APPENDIX III: DISPERSED SPORES: REGISTER OF ILLUSTRATED SPECIMENS

Figure	Slide		Negative	England finder ref. (Zeiss Photomic.)	GSC Type specimen No.
12a	SUNY Binghamton-	2002-M-32	PY 1397	S41/4/T42/1	103908
12b		'	PY 1399	'	'
12c		'	PY 1397	'	'
12d		2002-M-13	PY 1431	H53	103909
12e		'	PY 1430	'	'
12f		'	'	'	'
12g		2002-M-32	PY 1401	M63/4/M63/1	103910
12h		'	PY 1400	'	'
12i		2002-M-14	PY 1436	L54/3	103911
12j		'	PY 1438	'	'
12k		2002-M-22	PY 1415	P47/4	103912
12l		'	PY 1416	'	'
12m		2002-M-21	PY 1428	G49/4	103913
12n		2002-M-32	PY 1396	L38/2	103914
13a	GSC	329/24/T/21*	PY 1792	(175 1146)*	103915
13b		'	PY 1798	(244 1146)*	103916
13c		'	PY 1796	(233 1172)*	103917
14a		A-008058/22	PY 1556	W27/4	96756
14b		'	PY 1557	'	'
14c		A-008057/22	PY 1658	M51/3/N51/1	96757
14d		'	PY 1654	'	96758
14e		'	PY 1655	'	'
14f		O-95530	PY 1772	U64/1	103918
14g		A-008057/22	PY 1662	E48/4	96760
14h		'	PY 1664	'	'
14i		'	PY 1663	'	'
14j		A-008058/21	PY 1554	X43/4/X44/3	96761
15a	GSC	A-007132/21	PY 1742	066/4	96762
15b		'	PY 1743	'	'
15c		A-007132/22	PY 1749	M/39/4	96763
15d		'	PY 1748	'	'
15e		'	PY 1747	'	'
15f		A-007132/21	PY 1739	M48	96764
15g		A-007132/22	PY 1744	L40/3	96765
15h		'	PY 1746	'	'
16a	GSC	O-096385/x	PY 1676	Q38/R38	103919
16b		'	PY 1678	'	'
16c		'	PY 1691	X40/4	103920
16d		'	PY 1692	'	'
16e		O-96376/21	PY 1766	V58/4	96766
16f		'	PY 1769	D29/4/D30/3	98377
17a	GSC	O-096385/H-1	PY 1730	S62	103921
17b		'	PY 1733	Y63/3	103922
17c		O-96376/21	PY 1762	T30/2/S31/3	96767
17d		'	PY 1764	'	'
17e		A-008104/11	PY 1783	R44/4	96768
17f		A-008104/9	PY 1779	K46/4	96769

Negatives are held at The Natural History Museum, London. All specimens are housed in the National Palynological Type Collection of the Geological Survey of Canada in Ottawa. (* Oversized slide; coordinates refer to Zeiss photomicroscope II, number 65800, not England finder Ref.)